THE EPIPHYTIC ORCHID: LIFE ON A SHAKY LIMB

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It's strange to imagine, but it's true: Trees and plants are able to move. Though the process is gradual and a natural part of plant migration…, some species of trees may now be moving at a speed of roughly 100 kilometers a century.
- Daksha Rangan

PLANTS CAN MOVE, and orchids did. One of the great migrations of life occurred around 65 million years ago when orchids left the ground and started their trek to the canopies of trees. Imagine that! With their dust-like, innumerable, and mobile seeds, they left the storehouse of water and nutrients that is the earth and moved up to start a perilous life clinging to shaky limbs. The vertical journey had many advantages as well as a lot of trade-offs. True, there is more light in the canopy than on the forest floor. There are fewer herbivores and flightless predators. There is abundant real estate to inhabit with abundant niches. Above ten linear feet of the forest floor, there can be as much as ten times that amount of growing space on the branches and trunks of trees, rather like an apartment house. There is some protection from forest fires that rarely burn that high.

Yet, imagine the challenges. Bark sheds, limbs break, and trees eventually die. Pollinators can have a hard time finding you. Nutrients are often rare, and moisture is often scarce. Even after a downpour, the environment can be drier in some forest types than in the driest desert. High and dry—that is life as an epiphyte.

This is the remarkable story of how orchids managed to survive and thrive as plants that grow on top of other plants like tree trunks, branches, and even twigs. Zotz (2016) defines epiphytes as "plants that germinate and root non-parasitically on other plants at all stages of life." The roots are rigidly attached to the tree but do not penetrate or harm the tree. However, epiphytes occasionally grow on rocks or soil, and sometimes a terrestrial plant may "accidentally" grow on a living host; lines sometimes blur between epiphytic and terrestrial plants. As we hobby growers know, cultured seeds of

Epiphytic orchid.

many obligate (have to grow that way) epiphytes produce healthy plants on artificial soil mixtures, so there is really nothing mandatory about being anchored in a living tree canopy, if all needs are met. Orchids happily grow on fences and telephone poles. *Rhipidoglossum millarii* has been found growing on termite mounds, and *Cyrtopodium paniculatum* has been found growing on the fourth floor on the outside of an office building in a big city! The main point of the epiphytic life strategy appears to be an escape from competition and light limitation on the ground.

Catasetum macrocarpum

Tree crowns were only recently colonized, geologically speaking, by flowering plants like orchids. Why didn't orchids migrate to treetops sooner? The earliest trees were gymnosperms like the conifers, and their crown architecture, bark characteristics, and needles made them poor hosts for epiphytes. Orchids had no choice but to grow on the forest floor or elsewhere in the ground. The modern rainforest, home to so many epiphytes today, only started to develop about 65 million years ago in the Late Cretaceous period. Increased tree structural complexity and tropical climate boosted the conquest of tree crowns by plants like ferns and orchids. Flowering trees, the angiosperms (Magnoliophyta) arose and provided lots of space for plants to grow, and the age of the epiphyte began. While many epiphyte ancestors started as forest floor dwellers, many believe that a large number of epiphytes today inhabited savannah grasslands near the forest perimeters and started to climb on the shoulders of their neighbors to hoist themselves up into the newly-opened niches in the trees.

Today 10% of all vascular plants live as epiphytes. Epiphytes are found in many plant groups, including aroids, begonias, bromeliads, heaths, nightshades, orchids, ferns, and true mosses. That amounts to about 28,000 vascular plant species that always or mainly make their living in tree crowns rather than on the ground, but orchids are more successful than any other lineage. Around 68% of epiphyte species are orchids, and 70% of orchids live in tree canopies. Simply put, most epiphytes are orchids, and most orchids are epiphytes.

Virtually all epiphytic orchids are found in the Epidendroideae, a subfamily of plants in the orchid family; fewer than 100 epiphytic orchid species are known in all the other orchid subfamilies combined. Although sometimes found in near-desert conditions where fog is almost the only water source, epiphytes are most abundant in tropical rain and cloud forests. The air is constantly saturated, and the leaves drip from condensing mist. The humid environment allows the plants to obtain water and nutrients from the dust and moisture in the air and dampness and debris on their hosts.

Orchids have several adaptations that help them flourish as epiphytes. Their roots are covered with super-absorptive tissue called velamen that quickly sucks up scarce water and nutrients. Their leaves often have thick, waxy cuticles that slow water loss. They can use CAM metabolism (Crassulacean Acid Metabolism) for photosynthesis that allows them to keep their stomatal opening closed during the day to prevent water loss. They grow very slowly and generally are small, perennial plants, lowering their metabolic needs. Many have pseudobulbs which act as canteens to store water for the dry times. If they grow on twigs, they often reach sexual maturity very quickly. Moreover, many have deceptive or specialized pollination systems to promote reproductive success. The plants frequently have inflorescences that are pendent, hanging down off branches. With their toolbox of tricks, these orchids are truly a wonder of evolution.

Cyrtopodium paniculatum

Lianas, ferns, and moss covering a tree trunk in Brauli Carrillo National Park, Costa Rica.

Phorophytes

An epiphyte, by definition, needs to grow on the support of a host, most often a plant or tree, and that support is called a "phorophyte." Most phorophytes host various different types of plant families, genera, and species, a whole community living on and in an individual tree. In 1977, Valdivia studied 153 vascular species in 45 different trees in east-central Mexico. Only *Acacia cornigera,* which ants fiercely defend, had no epiphytes. The remaining 44 each hosted more than one epiphytic species, with the record being a tree that hosted 107 different species. The highest number of epiphytic taxa on a single tree ever reported is 190 species, growing on a 96-foot *Ficus cassiuscula* (family Moraceae) in a Peruvian rain forest. That is not 190 plants growing on the one *Ficus* but 190 different SPECIES. The second and third highest reported were 126 species in Costa Rica and 83 species in Bolivia.

Orchids are rarely monospecific, but the range of trees that they inhabit is often narrow. In a study of 105 epiphytic orchid species, about 40% associated with fewer than five kinds of phorophytes among 132 tree species available, and their biases all differed. Phorophyte bias during germination may have to do with the mycorrhizal fungi growing on the bark, the crown chemistry, or the degree of shade, all needed for successful germination. In the Philippines, trees chosen for germination were noted for finely canalled bark with numerous scales persisting for a long time, suggesting that rainwater debris in such shallow crevices might enhance seed attachment and the nourishment of seedlings.

Some orchids are so finicky that only one type of phorophyte will do. For example, *Zygopetalum maxillare* is restricted to tree ferns in wet and shady conditions in Brazil and Paraguay. *Dendrobium falcorostrum* is always associated with *Nothofagus moorei* (family Nothofagaceae) in Australia, while *Laelia speciosa* is ex-

Zygopetalum maxillare

Polystachya johnstonii

clusive to *Quercus deserticola* (family Fagaceae) in Mexico; the seedlings germinate on lichens that cover the host oak stems. *Constantia cipoensis* will only grow on *Vellozia piresiana* (family Velloziaceae) in Brazil, while *Polystachya johnstonii* grows exclusively on *Xerophyta splendens*, another member of the Velloziaceae family, among eight potential phorophyte species in Malawi. Moreover, large epiphytes like *Grammatophyllum, Coelogyne*, and *Cymbidium* species, common on *Dipterocarpus oblongifolius* (family Dipterocarpaceae), seem to avoid *Saraca indica* (family Fabaceae) in Malaysia. There are several more of these phorophyte-specific orchids that have been observed.

Orchids tend to grow best on parts of the trees that collect organic debris and water, such as the inner branches. Orchids' preferences for particular trees may have something to do with their water-holding ability and the niches they offer for drought-tolerant or moisture-loving species. Harshani et al. (2014) made aqueous extracts from the bark of tree species that were successful and unsuccessful phorophytes. They found chemically enhanced seed germination and growth of a mycobiont (fungus used by orchids to germinate or grow) in phorophytes, whereas extracts from non-phorophytes were inhibitory.

Orchids are often widely scattered, with relatively few individuals in each colony, 1.4 on average on each phorophyte. Mysteriously, some trees that seem acceptable have no epiphytes. Older trees offer weathered bark with more colonization by water-holding lichens and mosses and a larger, wetter surface area for a more diverse and populous orchid flora. Older and bigger trees make more desirable hosts. Epiphyte load shows a positive correlation to tree height and diameter, and epiphyte diversity and trunks usually expand together. Conservationists know that preserving the oldest trees conserves the most orchids and other epiphytes.

Laelia speciosa

Dendrobium falcorostrum

Some orchids prefer trees for their water-holding ability.

A catasetum in the southern Ecuadorean highlands.

Dendrobium chrysotoxum

Tree "Soil"

People often wonder how an orchid can grow on a bare tree branch. Surprisingly, trees often contain rich arboreal "soil." Succession on branches of a young tree often begins with lichens and bryophytes (mosses and liverworts) that result in a moisture-retaining, living mat that sets the stage for plants like ferns and orchids. Often overlooked is the fact that soil is not limited to the ground alone. Arboreal "soil" is often as rich as on the ground with mosses, lichens, rotting wood, suspended humus, ant nest gardens, and animal by-products providing a thick layer of debris, especially in older trees. The South Florida cypress tree's bark in better-nourished trees experimentally yielded potassium and phosphorous levels five to seven times higher and nitrogen levels three times higher than on the ground. Material removed from under epiphytes in the branches of *Swietenia macrophylla,* commonly known as mahogany, yielded 12 different cyanobacteria, at least two of which could break down or fix nitrogen. In an abandoned *Theobroma* cacao plantation in Ecuador, a comparison of five canopy media that supported many epiphytes showed that the canopy media compared to the ground below had more nutritive ions and a preponderance of nitrogen. Nadkarni (1984) also discovered several essential ions in the suspended humus in a Costa Rican cloud forest. Luckily for orchids, the densities of harmful mites, adult beetles, insect larvae, collembola, amphipods, and isopods (like woodlice) are far lower in the trees than on the ground.

A Phorophyte Changes With Time

It is interesting to note that a tree is not a static support. The surface expands from year to year while the limbs of the tree thicken. An epiphyte fixed on the bark surface is subjected to constant changes to which it must adjust over the years or die. There are important changes in the chemistry of the bark, in the available light and shade, in the position in the crown, and in the humidity available as the tree matures. Rasmussen (2018) claims orchid colonization of a tree is only successful when the whole orchid's life cycle is completed. A tree species or crown might enable seeds to germinate but not to flower. The orchid seedling may have germinated on a limb in the crown, but that limb changes and differs from the one on which the orchid is observed flowering years or even decades later. During the life of an orchid, everything in its habitat changes from irradiation to humidity to bark features to its neighbors on the branch. The orchid adapts, or the orchid perishes.

Epiphytes are usually thought of as not harming their host tree, but sometimes the tree is inadvertently harmed by its epiphyte load. The sheer weight of their mass can cause branch breakage and increase tree fall. Some host trees shed their rough bark periodically to prevent the overgrowth of orchids and other epiphytes. Some researchers feel that by absorbing nutrients quickly with their velamentous roots, orchids pirate nutrients and water that would otherwise have gone to the tree. It has been suggested that the fringing skirts in some tree ferns and palms protect against climbing epiphytes.

Pseudobulbs

One of the vital drought adaptations of many epiphytic orchids is the swelling of the stem, called a "pseudobulb." This organ acts as a "canteen," which stores carbohydrates and water for periods of drought. The presence of the pseudobulb facilitates a slow reduction in the water content of the leaves and helps mobilize water and carbohydrates under conditions of water deficit. It appears that water-soluble polysaccharides (glucomannans) can be mobilized from the pseudobulbs and transferred to the leaves via sucrose, where they contribute to leaf growth and maintenance. The loss of water reduces the photosynthetic capacity of the orchids and is associated with this emergency mobilization of water and sugar stores in the pseudobulbs. This "camel's hump" type organ enables the orchid to tolerate stress for a relatively long time.

Many epiphytic orchids, but relatively few terres-

Dendrobium crystallinum

Dendrobium officinale

trial species, have pseudobulbs. Pseudobulbs are found in roughly half of all genera in the Epidendroideae subfamily and are largely absent in the basal clades of the subfamily. The appearance of pseudobulbs coincides with the shift from terrestrial to epiphytic habit.

Yang *et al.* (2016) studied four dendrobiums and found that two coped with water scarcity with a thickened leaf cuticle, and two coped with a more thickened pseudobulb. The thick leaf cuticle of *Dendrobium chrysotoxum* and *Dend. officinale* conferred more efficient protection against water loss. Under water stress, the relative water content of leaves and pseudobulb decreased significantly but was still at a high level. Leaves of *Dend. chrysanthum* and *Dend. crystallinum* with thin cuticles lost more water through their leaves. They utilized their thick pseudobulbs with high water storing capacity to maintain water balance.

Dendrobium chrysanthum

Miltonia spectabilis var. *moreliana*

Roots

Orchid roots have superb adaptations to overcome the problems of the epiphytic lifestyle. Orchids growing precariously on branches at the top of the forest canopy are desperate for a secure hold, water, and essential nutrients. Orchid root structure helps solves these problems by quickly absorbing and retaining water and nutrients. Moreover, these roots exploit fungus to provide the plant with whatever the environment lacks. While most terrestrial roots are hidden in the soil, epiphytic orchids have aerial roots that hang down like long beards, exposed to the air or growing along the surfaces to which they are attached. The rich development of adventitious roots (roots that develop from non-root tissue like stems) allows anchorage when exploring the three-dimensional host trunk and branches. Thick, smooth, and silvery-white in color (except for the green or orange growing tips), the roots are covered with a layer of dead, air-filled cells known as the *velamen radicum*. The velamen thirstily soaks up rainwater like blotting paper, becoming transparent, revealing the green core of the root within. The spongy, outer velamen commonly has root hairs which occur only on the side of the plant facing the substrate to help in anchoring the plant.

The first few moments of rainfall have been shown to contain the most nutrients. Orchids need to soak up this precious water quickly. Gerhard Zotz and Uwe Winkler did a series of experiments that showed that dry velamen quickly captures this water. Within 15 seconds, the roots of the 11 orchid species tested were almost fully saturated. Within a minute, they were fully saturated. In contrast, water loss from a different set of ten orchid species' velamen was extremely slow, taking several hours. *Miltonia spectabilis,* with the thinnest velamen, took one hour to lose the water stored in its velamen. *Phalaenopsis* Malibu, with the thickest velamen, had lost about 50% in that time. Thicker velamen retained much more water after an hour.

The velamen acts as temporary water storage, allowing more time for absorption through the passage cells, maximizing intermittent rainfall. The velamen becomes almost impermeable when it dries out. Empty air-filled velamen cells slow water loss while fibrous caps above the passage cells also restrict water loss. As Benzing (1990) notes, "Should rain be scanty over long intervals or roots hang free or cling to non-absorbent bark in wetter sites, a large velamen dead space that prolongs contacts with precipitation could be crucial to survival." It has been noted that tropical orchids have thicker velamen layers than temperate orchids because topical orchids tend to be epiphytes and benefit from thick velamen in that dry environment. A tropical orchid like *Stanhopea lietzei* or *Catasetum fimbriatum* can have up to 15 cell layers of velamen.

Experimenters have shown that velamen also aids in nutrient retention. Since the last storm, the first rainfall has the most solute concentrations that wash off whatever nutrients have accumulated in the tree. These solutions often surpass those which are found in ground solutions. More than half the annual wet deposition of several nutrient ions fell on a dry Honduran forest within a ten-day rainy period, so the ability of the velamen to quickly take advantage of this bonanza is a real advantage. Like negatively charged phosphate, charged particles are retained in the velamen, probably due to positive charges in the velamen cell walls. Another study by Martin Tranier showed that aerial roots of phalaenopsis could absorb large amounts of nitrogen from urea and ammonium directly through the velamen.

Velamen also has special cells for gas exchange, absorbing oxygen for respiration, and, where chloroplasts are present, carbon dioxide for photosynthesis. (Because of this, loose, high porosity potting mixes like fir bark for the home orchid grower are recommended to make sure that the roots are bathed with air. When potting mix gets old, breaks down, and becomes anaerobic, the roots can "smother," deteriorate, and die.) It has also been suggested that the white color of velamen helps prevents overheating by reflecting heat. Velamen is a fabulous tool in the fight to survive as an epiphyte.

Velamen is not just confined to epiphytic orchids, and there are numerous terrestrial orchids with velamen. It has been suggested that terrestrial velamen pre-adapted orchids to move into the epiphytic niche when it became available due to its ability to maximize scarce available water. Several families besides orchids are equipped with velamentous roots, including some in the aroid genus *Anthurium.*

There are significant differences between terrestrial and epiphytic roots. Epiphytic roots are exposed to air and light. They are usually photosynthetic, perennial, tough, fairly consistent throughout the year, and long-lasting. On the other hand, roots of terrestrial orchids are usually non-photosynthetic, live less than three years, and often show seasonal differences. They are usually buried in soil or leaf litter, while epiphytic roots are most often aerial. In addition, terrestrial orchid roots are much more dependent on fungus living in their roots than are epiphytic orchids.

Lichen and mosses often provide wet cover for orchid roots. Lichen covers the roots of many orchids, and wet moss drips water around the roots of several others.

Fungus

Velamen is not the only root adaptation for survival. The ability to attract and digest mycorrhizal fungi is another vital epiphytic root adaption that allows the orchid to access extra food, nutrients, and water in a challenging environment. Orchids lure fungi into their roots, rob them of water and sugars, and then eat them up, giving little or nothing in return. Mycorrhizal infection is a universal feature of the Orchidaceae. Mycorrhizae are divided into ectomycorrhizal and endomycorrhizal fungi. The ectomycorrhizal fungus has threads that form a sheath around the root but do not penetrate the cell wall, while the endomycorrhizal fungus has threads that penetrate the root cell wall and grow in intricate coils.

Stanhopea lietzei

Catasetum fimbriatum

During some life stages, such as germination and seed growth, the orchid relies entirely on fungi for growth. At other stages, the orchid may use both fungi and light-based nutrition, sometimes supplementing one with the other. The fungi are a nutritional pipeline for the orchid.

Epiphytic orchids are 100% dependent on fungi for seed germination and growth. Orchid seeds are as light as dust and can pack four million of them a single capsule. Light and mobile, they have floated on air to colonize the world. Their lack of endosperm (food for the developing embryo) allows them to be this small and successful, and their association with fungi gives them the advantages of big seeds with little cost. In the orchid, fungi take over the nutritional role of endosperm in other plant families, and with fungal nutrition, there really IS a free lunch for orchid seeds. Water has been seen to drip from the end of hyphal threads, and the fungi provide not only food but water to the little seedling before it develops roots.

As adults, epiphytic orchids generally are less dependent on their mycorrhizal partners than are terrestrial orchids. Roots of northern temperate terrestrial orchids, such as in *Dactylorhiza purpurella,* show almost

Epidendrums covering a branch in a cloud forest in Panama.

complete infection soon after formation. Fungi are essential for terrestrial adult nutrition in a world with little open sunlight. In contrast, the root infection among adult tropical species is usually less dense and may be very sparse. The aerial roots of epiphytic orchids are not infected until they come into contact with a suitable substrate. Parts that remain aerial are usually not infected. Epiphytic orchids seem to be less dependent on fungi for survival, having more access to sunlight for food production.

A diversity of fungi has been associated with orchids, mostly isolated from the orchid roots. They are found in all seeds and protocorms and occasionally in rhizomes. The most common fungi include a heterogenous assemblage of mycelia referred to as the *Rhizoctonia*. These fungi are most often found in areas of the cortex below epidermal hairs, often close to the root tip. Passage cells in the root not only allow water and mineral entrance but are said to emit chemical signals for the attraction of endomycorrhizal fungi, allowing them to cross the root cortex. The fungal hyphae then reach and stay in parenchymatic cells, where peloton formation begins. When infected, the root tends to be relatively yellowish and opaque, and living pelotons are most often found close to the root's surface. These pelotons are loosely looped aggregations of practically transparent hyphae that are eventually digested by the orchid before they cause infection to the plant.

Fungi are not plants and cannot produce their food through photosynthesis. Instead, they break down dead organic material or attack or live on or within living organisms. There are estimated to be more than a million fungi species, at least six times more than any plant species. It is estimated that there can be 20,000 km (12,000 miles!) of hyphal fungus threads in one cubic meter or yard of soil. At 1/60th of the thickness of a normal orchid root, they can penetrate narrow and distant places that the orchid cannot, shuttling food and water to the orchid. Orchid roots typically are small, unimpressive, and relatively short, and the large fungal surface area greatly increases the volume of food and water available to the orchid.

Trash Basket Roots And Ants

Some orchids develop "trash basket roots," an entangled root system of erect basal roots to supplement nutrition in the poorly developed epiphytic habitat. This spectacular matrix of roots collects leaf litter and debris, nourishing the orchid. The spectacular upright roots are found in several orchids like *Ansellia africana, Grammatophyllum speciosum*, and *Coryanthes macrantha.* In some of these plants, extrafloral nectar is also secreted on new shoots, bracts, and the outer surface of orchid buds, which attracts ants that nest in their roots. The ants collect vertebrate feces that fertilize the orchid, and they aggressively defend the nest. The ant gardens grow epiphytically and consist of masses of soil, detritus, and chewed plant parts, all assembled at the

Ansellia africana with upright roots.

branches of the trees. All orchids in these partnerships are highly adapted, mostly obligate (only existing in one environment) ant-garden plants.

Coryanthes is a genus that grows exclusively with these so-called "ant gardens" in their roots. The balls of roots can grow to five feet (150cm) in diameter, with the ant nest itself comprising 31 inches (80 cm). Both organisms share a common destiny because the *Coryanthes* is thought to die if the ant colony dies. The ants provide herbivore defense and debris nutrition, and the orchid provides a root framework for nest construction and extrafloral nectar. Ant-provided nutrition allows rapid plant growth. Flowering in only two-to-three years from seed, an orchid record, *Coryanthes* produce massive flowers, each weighing more than three ounces (100g), the most massive individual orchid flower. Capsules containing 600,000 seeds mature in only two months. Many orchid genera have species whose roots may be occupied by ants—*Gongora, Grammatophyllum, Vanda, Cattleya, Dendrobium, Coelogyne, Vanilla, Arundina, Oncidium*, *Spathoglottis*, and *Myrmecophila.*

The genus *Myrmecophila* is intimately associated with ants; they were formerly part of the genus *Schomburgkia.* The hollow pseudobulbs have a slit through which a mated queen ant enters and lays her eggs, establishing her colony. The home is called a "domatia," and the ants will protect the *Myrmecophila* in exchange for food and shelter.

The orchid gives it nectar, and the ants act as fierce bodyguards, preventing herbivore attack. The ants pack the pseudobulbs with dead ants, parts of their meals, and poop, and radioactive studies have shown that the orchid can access nutrition from the domatia.

A number of orchids regularly root in the carton nest construction of arboreal ants. They also produce myrmecochores (seeds with nutrition for ants), some with conspicuous edible appendages, that promote dispersal from established to developing ant gardens. Carton is a composite material that can be quite nutritive if it contains soil, feces, or honeydew. Carton ant galleries crisscross much bark surface in some Amazonian forests, allowing orchids contact with nutritious ant products.

Leaves: Drought Avoiders and Drought Endurers

Orchid leaves have developed two different approaches to overcome extended periods between storms that an epiphyte must endure, being a drought avoider or being a drought endurer. Drought avoiders are seasonal growers that restrict their vegetative growth to wet times. These yearly cycles of wet and dry require special adaptations. These thin-leafed orchids drop their leaves during the dry season and go into dormancy, a deep sleep where water is not required. Growers of plants like catasetums, a drought avoider, don't water these orchids during the winter.

Epidendrum secundum

Trichoceros onaensis

The carbohydrates and water are stored in their fat pseudobulbs, and rapid growth resumes when favorable weather returns. Most of the Catasetinae and certain lycastes and dendrobiums are drought avoiders.

Drought endurers, like cattleyas, sustain themselves in dry periods by using the energy and water stored in their pseudobulbs. Their leathery, succulent leaves, stout, durable roots, and velamentous and photosynthetic roots enable them to endure the dry season. (Some epiphytic orchids like phalaenopsis do not have pseudobulbs and rely on fat roots and leaves for energy and water storage,)

Drought endurers use thick leaves to cope with their arid environment. Their leaves are generally more rigid with a thick, waxier cuticle and no prominent veins. They have thickened epidermal cells with a stiff cutin layer, extensive lignification (woody cells), and layers of strong sclerenchyma fibers. Such leaves will usually snap or crack when bent beyond a certain point. Their mesophyll has fewer chloroplasts, is adapted for water storage, has larger cells and more cell layers. They are most often "conduplicate," which means they have two flat halves folded once along their middle. Sometimes the leaves are arranged so that rainwater is channeled into the base of the plant, watering the roots from above. They are meant to capture and store as much water as possible in their fleshy leaves and lose as little as possible through their thick, waxy cuticles.

CAM Metabolism

Carbon dioxide (CO2) uptake, essential for photosynthesis, and water loss occur through the same stomatal openings. Most plants open their stomata during the day, even though this causes a loss of more than 90% of the water absorbed through the roots. Epiphytic stomata are often fewer in number and recessed. Epiphytic orchids often use a specialized adaptation called Crassulacean Acid Metabolism (CAM) to minimize water losses. Carbon dioxide is absorbed during the night when stomata are open and then stored within the leaf vacuoles in the form of malic acid for subsequent photosynthesis during the day when the stomata are closed. Closing stomata during the day and opening them at night minimizes water loss.

The intermediate storage of carbon dioxide as an acid has an energy cost, however. CAM plants like orchids grow relatively slowly and often take a long time to mature. The more succulent the orchid, the more likely it is to use CAM. Thick-leaved cattleyas and phalaenopsis often use CAM metabolism, while thin-leaved oncidiums often use the more conventional photosynthetic pathway. Some species, like *Dendrobium officinale*, can alternate between CAM and C3 depending on environmental conditions. Orchids alone account for almost half of all CAM plant species globally, with about 8000 taxa. The only known terrestrial orchids with CAM are in the Eulophiinae subtribe, comprised of nine genera

Telipogon vampyrus

Gongora armeniaca

with 270 species. CAM is not a prerequisite for the epiphytic lifestyle, but it is a very helpful adaptation.

Pollination Strategies

Being an epiphytic orchid presents unique problems when it comes time to reproduce. Populations are often just scattered individuals or small, extensively dispersed clusters. The relatively small size of epiphytic orchids may limit flower production, and the floral display may not be sufficient to compete for pollinator attention. To cope, these orchids employ one of several specialized pollination strategies which involve deception or exclusive or unique rewards. As Ackerman (1986) says:

> Epiphytic flowering plants possess an incredible array of morphological, anatomical, and physiological adaptations associated with the stresses imposed by their habitat… Does the epiphytic habitat impart unusual constraints on plant-pollinator interactions? If so, then how do epiphytes cope with these conditions?

Deceptive pollination systems occur in one-third of orchids as a coping mechanism in both epiphytic and terrestrial orchids, and little or no reward is offered to the pollinator. Now there is a "triple whammy"—widely dispersed flowers, small floral displays, AND no reward. What is an epiphytic orchid to do?

Some resort to the common deception of mimicry to attract a pollinator. Batesian mimicry involves an orchid mimicking a rewarding flower that is common in the vicinity, a "magnet" that attracts pollinators who are fooled into thinking the orchids are one of the other rewarding flowers. For example, the epiphytic species *Warczewiczella lipscombiae*, which offers no rewards, attracts bee pollinators because of its shared floral appearance with the trap lining liana, *Clitoria javacensis (*Fabaceae) that does offer rewards.

Epidendrum secundum also invites butterflies to dinner by resembling rewarding species. This species is similar in color forms and overlapping habitats with *Asclepias curassavica* (Apocynaceae) and *Lantana camara* (Verbenaceae), both of which produce nectar. Hummingbirds, butterflies, and skippers are misled and do the orchid's reproductive work with no reward. This type of deception where two or more rewarding species resemble each other is called "guild mimicry."

Another example of this mimicry is performed by many large-flowered, nectarless dendrobiums that deceive bumblebees by mimicking rewarding rhododendrons. In India and Sundaland, the mass flowering of rhododendrons at the tops of trees alerts honeybee sentinels. The dendrobiums bloom concurrently with a mass blooming of their own. This "feeding frenzy" gets nectarless dendrobiums pollinated as part of the excitement.

Some epiphytic orchids rely on the naivete of young insects by their general resemblance to rewarding flowers. In the Himalayas, the newly-emerged queen bumblebee, the only survivor of her colony, emerges in the spring before the rains begin and starts gathering nectar and pollen for her growing brood. It takes two to four flights for her to learn that the orchids have no nectar, and many dendrobiums manage to get pollinated during this learning curve.

Some insects are attracted to orchids because of their supposed resemblance to insect brood sites. During the visit, the insect may pollinate the flower. For example, fungus gnats like to lay their eggs on fungus and are attracted to anything mushroom-like. Vogel (1978) collected examples of fungus-mimicry in the genus *Masdevallia (*those that now belong to the genus *Dracula*), where the lip of the flower had a horseshoe shape and radiating gill-like ridges on the side that faced downwards just like a mushroom. Pollination often occurs during egg-laying. Of course, the orchid is not a good site for developing fungus gnat eggs, but the orchid has been served.

Sexual deception, although more well-documented in terrestrial orchids, also occurs in some epiphytic orchids. Perhaps the most bizarre sexual deception involves male insects who are so aroused by the scent, look, and feel of an orchid that they try to mate with it. Called "pseudocopulation," it is only false for the insect; it is real for the flower. During the insect's frustrating amorous attempts, pollinia are picked up and

Dimerandra emarginata

delivered, and orchid sex is completed. Apart from ten epiphytic species from Japan and the Americas, all sexually deceptive orchid species are terrestrial. However, the epiphytic *Tolumnia henekenii* called the "Bee Orchid" (now severely endangered) does this trick by resembling a fuzzy bee with a head, legs, and wings, making it irresistible to amorous male bees. It is found in Haiti and the Dominican Republic in dry brush and cacti in arid, subtropical forests. Epiphytic trichoceros and telipogons also use sexual deception to attract pollinators.

In the Neotropics, about 600 species of orchids, mostly epiphytic and some terrestrial, produce floral fragrances as an attractant and exclusive reward for male bees. Exotic fragrance, bizarre flowers, and complex pollination mechanism attract male bees who store the fragrance compounds in their back legs and then convert the chemicals into sex pheromones. The best known are the Stanhopinae like *Stanhopea*, *Coryanthes*, and *Gongora* and the Catasetinae like *Catasetum* that use volatile chemicals to attract specific species of pollinators. The epiphytic *Coryanthes speciosa* and some of its cousins have very bizarre lips that look like a bucket or swimming pool with liquid dripping from the side of the column like a faucet topped by a helmet covered with slippery, fragrant waxes. Euglossine male bees collect these waxes with their feet to make an aphrodisiac to attract their females, appear to get drunk, and slip into the wet bucket, escaping by climbing a ladder of hairs in the back of the flower. Exiting, they pick up and deposit pollinia. Euglossine bees have long lives and forage over long distances, and this, and their fidelity, makes them excellent pollinators. As we can see, epiphytic species with small floral displays and scattered populations successfully use specialized floral attractants to enhance their reproductive success.

Many epiphytic orchids can also reproduce vegetatively.

Twig Epiphytes

Finally, twig epiphytes are a special case with unique adaptations. Twig epiphytes are the brave, tiny orchid plants that spend their lives on a little twig. It is a most inhospitable place for an epiphyte, but they have learned to make a living and thrive in this hostile environment. Their small size allows them to make use of this short-lived habitat in the canopy. They have unique adaptations like protuberances of the cell wall, modified cells in the velamen of the root, and hooks on their seeds that allow them to take advantage of the smooth bark of many twigs. Perched precariously on fragile twigs or even on leaves, they receive a lot of sunlight, low humidity, and a low accumulation of minerals. They have scant substrate with limited absorbent capabilities. Many have clinging roots with one or more secondary points of attachment to increase the number of seasons before they are shed. The host can often be found with several twig epiphytes dangling loosely by their clinging roots. They often have laterally flattened leaves that are unifacial or absent, increased root production, and limited shoot development.

Twig epiphytes display many characteristics of weedy plants. In constant danger of blowing or falling from the tree, they have a high mortality of juvenile plants, and a large number fall off the trees and shrubs on which they grow. To compensate for living on the edge, they have incredibly fast growth that allows them to reach sexual maturity by one year. (In contrast, an epiphyte like *Dimerandra emarginata* takes six to ten years to mature sexually.) This fast growth gives them the greatest chance of reproducing before they fall off the twig or land with the broken twig on the ground.

Erycina crista-galli and *Ercn. pusilla,* like all *Erycina*, are twig epiphytes, and they grow abundantly in coffee plantations, aided by their rapid growth. The coffee bushes, pruned annually and replaced every four or five years, are home to these orchids that have evolved to live life at top speed and specialize on this relatively ephemeral substrate with little or no competition from other orchids. Other genera that have adapted to growing on the twigs of coffee bushes are *Leochilus, Notylia, and Ornithocephalus*.

In the New World, twig epiphytes developed in some of the Oncidiinae and Pleurothallidinae. In Southeast Asia, they developed in some species of *Bulbophyllum* and *Taeniophyllum,* and in Africa, the habit occurs in *Microcoelia* and Angraecinae.

A suite of ingenious adaptations has enabled the orchid family to conquer the treetops and become the most successful epiphyte in the world.✾

Erycina pusilla

Leochilus labiatus

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Eulophia nuda

This genus has over 200 species and is distributed worldwide in the tropics and subtropics but predominately in Africa and continental Asia. (Pridgeon et al.) *Eulophia nuda* is a terrestrial orchid found in tropical and subtropical Asia to the West Pacific at elevations of 300 to 1,500 meters (984 to 4,921 feet). It is warm growing and blooms in the spring. The flower is extremely varied throughout its range. It is known for its ethnomedicinal uses by local healers in India. Grown by Harold Koopowitz.

Eulophia nuda