ALL THE DIRT ON TERRESTRIAL ORCHIDS

CAROL SIEGEL

WHEREVER YOU LIVE, there are challenges and opportunities. There are roaches in New York City but also lots of jobs. There are tent cities in Los Angeles but also wonderful weather. There are hurricanes in Miami but also beautiful beaches. Life is all about coping with the difficulties and exploiting the advantages of wherever you find yourself. Orchids are no different. The vast majority of orchids make a living clinging to tree branches or hanging from rocky cliff walls, but an estimated twenty-five persent of orchids grow in the dirt, just like most plants. They are called "terrestrial" orchids and face unique challenges and opportunities.

We are so accustomed to living on the ground that we forget what a special place the dirt beneath our feet really is. From ants to bees, desert tortoises to moles, earthworms to beetle grubs, much of life calls the soil home for at least part of its existence. Microscopic life flourishes in the dark soil, especially spectacularly vast networks of fungi vital to the orchid life cycle.

A giant sponge, the ground holds and stores vast amounts of life-giving water and nutrients. The presence of many other types of plants attracts vital pollinators, even when orchids give no reward. In difficult times, during fire, drought, or other stresses, when orchids can't or don't want to put up aboveground parts, they can shelter underground until times are better. They can feed from the vast underground fungal network and parasitize the rich resources it provides. Remaining dormant in the dirt, they burst into glorious bloom when the time is right. Many a researcher has thought an orchid extinct or lost in a location, only to discover years later that they were just under his feet, dozing in the dirt.

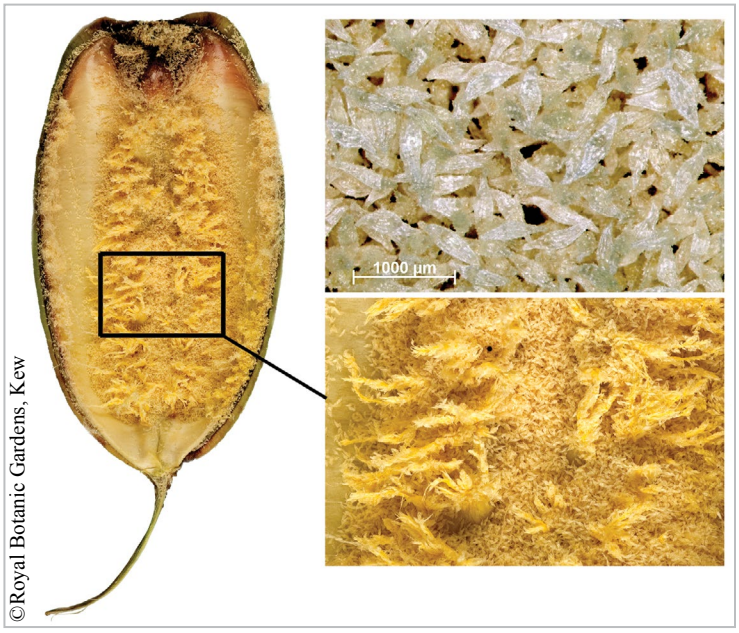
There are challenges, however. If you research "terrestrial orchids," hundreds of articles raise the alarm on how vulnerable terrestrial orchids are to extinction, especially due to climate change or human activities. Although only comprising a quarter of all orchid species, terrestrial orchids represent half of the extinct orchid species, according to the World Conservation Union (IUCN 1999). Their reliance on specialized pollinators and a narrow range of fungal types can make life in changing times very hard. Not only do the orchids have to be able to adapt to warm temperatures and changing weather patterns, but their fungal partners and pollinators have to adapt and be there for them as well. It's not always easy to be a terrestrial orchid these days. Grazing, changing mowing patterns, fire, and salinity all threaten declining terrestrial orchid populations. The loss of habitats due to agriculture, overcollection, and growing human populations present a special threat to terrestrial orchids, growing as they do in the ground.

Seeds: The Underground Phase

The unique first stage of terrestrial orchid life occurs underground, out of view, for weeks, months, even years, a stage from seed to germination to protocorm to first leaf. Germinating embryos develop into protocorms, the stage after germination when the seedling has a shoot tip with primordial leaves but no roots. Most hobby growers are oblivious to this important stage of orchid life. They only know or care about the leafy photosynthetic, blooming stage. Being out of sight, this sometimes very long underground phase, often lasting years, has been difficult to unveil and still has many secrets.

Terrestrial orchids differ from epiphytic orchids in their long underground phase and their need to be buried in the earth and to be dark before germination. This prolonged underground phase is only found outside of orchids in the subfamily Pyroloideae in the family Ericaceae (commonly known as the heath or heather family). Terrestrial orchids start life as the tiniest seeds in the world, no bigger than a grain of flour or a speck of dirt. Evolved to float on the wind and travel long distances, the seeds fill with air like tiny balloons, buoyant in both air and water. More resistant to water than the seeds of epiphytic orchids (those that grow on trees), some terrestrial orchid seeds can survive to germinate in bogs and near streams and can better resist the attack of microbes in the soil.

Incredibly light, the orchid seeds are estimated to be as much as a thousand times more numerous than those of any other plants. A capsule contains thousands, if not millions, of seeds, and a single plant can produce



Grammatophyllum speciosum seed.

many capsules. Very few seeds, however, survive to maturity. The survival of germinated seeds through the protocorm stage to the seedling stage is typically low. Rasmussen posits that the germination of some species is as low as one to five seeds per billion produced.

Seeds can travel incredibly long distances to deliver their genetic package; seeds of *Orchis simia* have been found 250 km (155 miles) from the nearest known seed source. Often, however, seeds settle to the earth just a few feet from the mother plant. Once they land on the ground, they do not immediately germinate. In general, extremely small seeds like those of epiphytic orchids germinate only under the influence of light, but terrestrial orchid germination is impeded or prevented by light. Many terrestrial orchid seeds require darkness and the very slow hydration of seeds to ensure that they will be completely buried before germination. Unburied, the seed might desiccate before germination in the ground. Only bog orchid germination is not impeded by the presence of light. The depth of seed burial of non-bog orchids before germination varies from *Anacamptis morio* at three to five cm (one to two inches) to *Orchis ustulata* at five to ten cm (two to four inches). Sometimes the seed is covered in leaf litter and humus, and sometimes it is washed down into the soil over time. Some seeds require a cold spell before germination, like *Corallorhiza odontorhiza,* where the longer the cold spell, the more seedlings germinate.

Because orchid seeds are so light, they contain just an embryo with a few cells and some limited lipid and protein reserves. Although the seed has these meager resources for beginning germination, no further growth can occur until the seed attracts a fungus and can steal its nutrients and water to develop a symbiotic relationship (mycotrophy) with the fungus. Water has

Anacamptis morio

Microscopic orchid seed.

Corallorhiza odontorhiza

Fungal hyphae

Corallorhiza trifida

been seen dripping from the ends of hyphal (fungal) threads, watering the orchid seedling during the early stages of life. Recruiting a suitable fungus is the crucial step in the orchid's life cycle and a universal feature of Orchidaceae. No one knows what prompts a fungus to invade the seed, only to be consumed by the host orchid over and over again. It is conceivable that fungi produce chemicals that assist in breaking physiological dormancy

It has been over a hundred years since Noel Bernard and Hans Burgeff realized that orchids are "married' to fungi. The fungi that infect orchids are called "mycorrhiza." During germination, the orchid depends entirely on nutrition from the fungus. Terrestrial orchids at other stages may use both mycotrophic and phototrophic nutrition (photosynthesis), either alternatively or supplementing each other in a wealth of combinations.

Orchids parasitize an astounding diversity of fungal families, which, as of 2015, included 35 fungal genera, referable to 22 different families, 12 orders, and two phyla. The largest recognized group of orchid fungi is a heterogeneous assemblage comprising mycelia referred to the form genus Rhizoctonia. Some orchids will only germinate with a specific fungal partner, while others are less specific. *Corallorhiza odontorhiza* needs a very specific fungus, whereas *Bletilla striata* is fairly unfussy in its choice of partner.

Unlike other angiosperm seedlings, the newly-germinated orchid has no radicle (the part of the embryo that develops into the primary root), but the suspensor end of the embryo specializes to form mycotrophic tissue for fungal nutrition. During their underground leafless, seedling stage, orchid protocorms are fully mycotrophic (completely reliant on fungi) and remain dormant in the ground for a considerable amount of time until they make contact with just the right fungus. The fungal threads or hyphae enter the protocorm through hairs or trichomes. Overall, the amount of time spent as a purely heterotrophic (fungus-dependent) seedling until the first foliage leaf above ground is thought to vary from three to four months to two to four years or more. The protocorm stage lasts for a varying amount of time. *Goodyera pubescens,* for example, has a protocorm stage lasting at least six months after germination.

Orchids That Never Grow Up: *Corallorhiza*

When we think of parasites, we think of leeches, wood ticks, and intestinal worms. Pretty orchids are the last thing we think of, but all orchids are parasites as seedlings, and many are sometimes parasites as adults. Relatively few orchids, about 170 species, show no traces of chlorophyll and remain parasitic on fungi their whole adult lives. Like the kid who never leaves home, they never make a living on their own. We call these orchids "mycoheterotrophs" (MH). For example, species in the MH genus *Corallorhiza* never develop functional photosynthetic tissue and parasitize soil fungi their entire lives. Eleven species of *Corallorhiza* are found mostly in the New World from Guatemala to Canada and also in Eurasia. The aboveground portion of the plant consists of a single leafless stem bearing five to twenty or more flowers. Except for *Corallorhiza trifida,* which is pale green, all the rest are brown, reddish brown, or purple because of anthocyanin pigments.

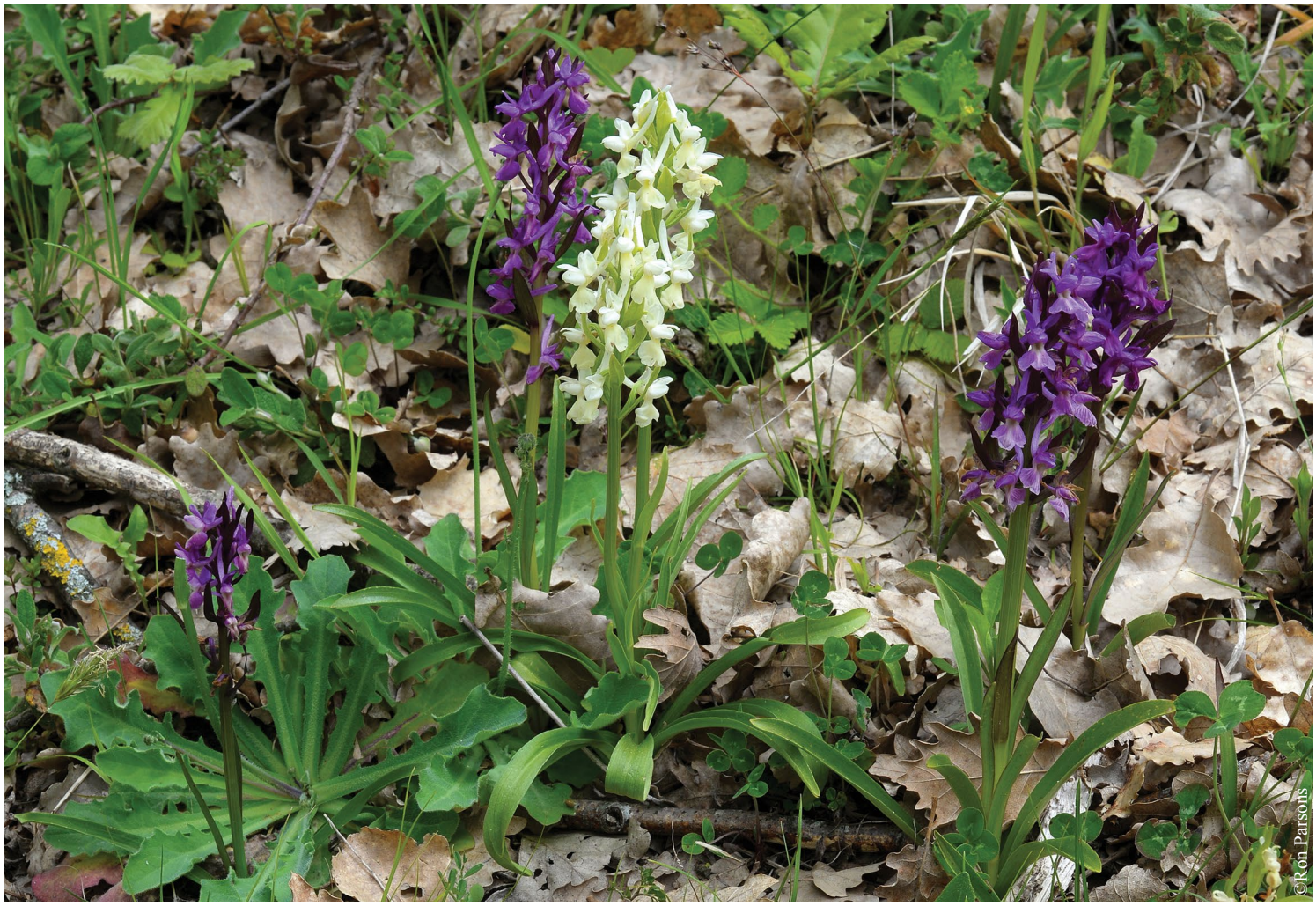
With no roots at all, *Corallorhiza* species rely on a subterranean rhizome (enlarged stem) system and hyphal threads to provide enough water to send up an inflorescence. They don't bother with roots at all, being heavily and permanently infected. Since the hyphal fungal threads are only 1/60th the diameter of a typical root and sometimes extend for miles, they form a very effective pseudo-root for the orchid. Some orchids like *Corallorhiza striata* have characteristic black rhizomes due to the presence of highly melanized fungi. Densely branched, a tiny scale leaf supports each section of the rhizome branch. Since the main axis is bent at the point where the lateral shoots come out, it is thought to resemble coral, and the pattern is called "coralloid," hence the name *Corallorhiza* or "coral root."

Epipogium, another MH genus, is called the "Spurred Coral Root." This is, of course, a misnomer since there are no roots at all, just a long-lasting swollen stem. One species, the widespread *Epipogium aphyllum,* is also called the "Ghost Orchid" since it spends most of its life underground and has a tendency to appear and disappear suddenly. It has a ghostly pale, waxy appearance with no green pigment.

Evidence points to the fact that *Corallorhiza* has only recently transitioned to obligate mycoheterotrophy. Only *Corallorhiza trifida, Corallz. odontorhiza,* and *Corallz. wisteriana* have an observably green color indicating the presence of chlorophyll and any possibility of carbon fixation through photosynthesis. Freudenstein and Barrett examined the *rbcL* gene, which codes for the protein RUBISCO, responsible for fixing CO2 in the dark reaction of photosynthesis. Once the transition to MH was made, rbcL became unnecessary. That gene and others related to photosynthesis have been lost from the genome or mangled so badly by repeated mutations that they are nearly unrecognizable. As a result, the plant, genetically, can no longer feed itself through photosynthesis. In the *Corallz. striata* and *Corallz. maculata* lineages, the gene is largely intact, but a number of mutations render it nonfunctional, indicating a relatively recent transition to MH. So this genus has changed both in genotype and phenotype, literally inside and out.

Epipogium aphyllum

Mycoheterotrophic plants with no chlorophyll characteristically exhibit high fungal specificity meaning they only grow with one or a few fungal partners. *Corallorhiza striata* and its complex are high on the scale of specificity toward fungi in the genus *Tomentella*, specifically *Tomentella fuscocinerea*. The species *Corallz. maculata and Corallz. mertensiana* exhibit high specificity toward the ectomycorrhizal (growing as a network on the outside of roots) Russulaceae fungi with no overlap in the fungi on which each species depends. Non-MH orchids seem to be much less specific in the kind of fungi they allow to infect them.



Dactylorhiza romana

The Mixotrophs: Sometimes I Eat at Your House, Sometimes at Mine

Seventeen plant families with some green members often don't bother with photosynthesis as adults and just tap into the "underground highway" of fungal nutrition when needed. Orchids are among these. Some green orchids can get as much as 90% of their carbon from fungal association. This is called having a "mixotrophic" habit in which plants obtain nutrition from their fungal partners sometimes but not always. *Limodorum abortivum* does not make enough food through photosynthesis and supplements its carbon supply by associating with ectomycorrhizal species. Its leaves are reduced to scales, and although it has some chlorophyll, there's not enough photosynthesis to fulfill its needs. (Interestingly, its seeds are among the largest produced by orchids, and seedlings develop very slowly, remaining entirely below ground eight to ten years before flowering.)

Epipactis microphylla is a green orchid that can perform photosynthesis, yet 78% of these orchids are colonized as adults by truffles, which are fungi that provide supplemental nutrition. Foragers can use the presence of *Epcts. microphylla* to hunt for truffles. Other *Epipactis* and *Cephalanthera* species also are used to indicate truffles.

The roots of mixotroph species in genera such as *Orchis, Platanthera,* and *Dactylorhiza* show "root dimorphism," visual evidence of their dual lifestyle. Their roots are organized into fat tubers with a special storage anatomy and slender mycotrophic roots to harvest fungal chemicals. They alternate between using light and fungal energy. The slender roots last less than a year, growing in the autumn or spring and dying down in the summer when leaves die back. The tuberous roots store energy for the following year's growth, allowing the plant to survive a leafless season.

Dactylorhiza orchids alternate periods of green leafy growth with seasons when they subsist on their tubers and root fungus; both the roots and tips of the tubers remain mycotrophic until spring when the new leaves emerge. Nitrogen content in the leafless plant increases by about 43% in winter, stored carbohydrates by 25%, and structural polysaccharides and fiber by 11% during which time they are totally dependent on fungi. Clearly, this is a mixotrophic orchid using both sunlight and fungi alternately for survival.

In *Platanthera chlorantha,* another seasonally leafless orchid, hyphae emanate from little "rhizoids" in parts of the root where pelotons (fungal coils) are alive. An adult plant has roughly 11,000 rhizoids that provide three times as much hyphal connection to the soil. These threads can rapidly proliferate in the event of

Platanthera chlorantha

local or sudden food shortage and exude enzymes to break down complex compounds in the soil, which the orchid can't do. In an emergency, the orchid can quickly switch to a largely fungal diet. Handy…

It is interesting to note that the particular strain of fungus that is important for germination of an orchid is often different from the one that the orchid uses in adulthood as an alternate source of nutrition. There are many variations on this orchid-fungus theme.

Orchids on Fire and Dormancy

One of the most striking features that distinguishes terrestrial orchids from epiphytic ones is their propensity for vegetative dormancy in many species. Because terrestrial orchids live in the dirt, they can easily retreat underground when needed. Adult plants may fail to produce aboveground structures during dormancy but remain physiologically active under the ground for one or more growing seasons.

One of the reasons why a large proportion of orchid collections are of epiphytic orchids is because few people are willing to wait a few years before seeing their orchids again! The inexperienced grower just thinks the plant is dead and throws it out. It is also true that most people find terrestrial orchid species next to impossible to cultivate or can only keep the plants alive for very short periods due to their obligate fungal relationships that are difficult to duplicate in cultivation. Many species are naturally short-lived as individuals, so harvesting from the wild for short-term gain is disastrous since this unsustainable practice depletes populations by not allowing plants to set seed.

Vegetative dormancy has been observed in species from 24 plant families, but it is unusual in these families. It has been noted that over half of the species in which this dormancy was recorded were orchids, and Shefferson said, "We are unaware of a terrestrial orchid species in which vegetative dormancy does not occur." (Shefferson et al. 2018) Plants as varied as *Thelymitra bracteata* and *Cypripedium reginae* regularly go dormant. In dry years, *Thel. bracteata* may not emerge at all. This entirely underground existence may last as long as 20 years in some species!

Remaining underground for years at a time is a successful strategy employed by orchids living in fire-prone areas in Australasia, South Africa, and Madagascar. In the Cape Floristic Region of South Africa, where the so-called "fynbos" vegetation predominates, orchids remain dormant underground for years and require fire to break dormancy at roughly eight- to twenty-year intervals. Many other plant families depend on fire to bloom, but almost half of these South African species are terrestrial orchids, by far the largest plant family there to depend on fire

At least 386 species of terrestrial orchids are thought to be fire-stimulated in Australia and South Africa alone, with peak flowering occurring within the first year or two after a fire and then subsiding to low or zero levels. The orchids often survive as tuberous geophytes (persisting underground), gathering resources, often symbiotically from mycorrhizal fungi in the soil, and protected from the next fire by a layer of earth. Their energy supplies are stored safely underground, waiting for the signal from the heat and chemical by-products of the next fire to grow, flower, and assure the next generation.

A striking example of this life history occurred in January 2000 on a rural road south of Cape Town when tinder-dry summer vegetation fueled a fire, whipped up by strong winds, that quickly ravaged out of control. Homes were lost, 8,400 hectares (20,757 acres) of vegetation were destroyed, and suburbs were covered with ash. Mountainsides were blackened, and devastation was everywhere. Yet within a few months to a year, a riot of orchids, often in blooming masses, colored the hillsides everywhere. As Hendrik van der Hoven stated (2002), "In some areas, it was hard to put down a foot without stepping on an orchid plant." Places where just a few orchids occurred before the fire now had orchids growing everywhere, including ones that had never been seen before.

There are some theories as to why fire breaks dormancy. Some believe that the ethylene gas produced by fire induces flowering. Others feel the heat of the fire may be a cueing factor.

Pyrorchis nigricans

Fire may activate flowering through karrikinolide, a plant growth regulator that occurs in plant-derived smoke and has been shown to trigger seed germination in many species. Flowering by orchids has been observed in unburned areas where smoke has only passed. One terrestrial orchid, *Pyrorchis nigricans* that had not flowered for 20 years bloomed when the ethylene-producing plant growth regulator ethephon was applied.

Another theory is that the increased light level due to biomass loss is a key reason for orchid regrowth. This influence lasts only two or three years after the fire, before the vegetation returns and the orchid flowering decreases. Nutrients released by the burned overstory of overlying vegetation coupled with warmth and moisture retention as an indirect effect have been hinted at. All these factors are thought to work together, and no single factor seems to be enough. Just pruning foliage or adding nutrients to the soil does not seem to mimic the effect of fire.

Thirty-four species of Disa are fire-stimulated to bloom. An unusual adaptation to fire is seen within *Disa* section *Monadenia* where *Disa ophrydea* has a dark, beetroot-red inflorescence and leaves that serve to camouflage the flowering plants among the skeletal remains of the burnt vegetation. The flowering stems and fleshy leaves of several species in the section *Monadenia* are sought as food by baboons, small antelopes, and rock hyrax. The dark, red-to-black cryptic coloration is thought to offer protection from these mammalian herbivores by helping the orchid blend into the scorched countryside. The flower color, however, is atypical for a moth-pollinated flower, and the orchid attracts its pollinator with its sharp cinnamon scent from dusk to dawn.

Rhizanthella Gardneri: Living Off the Neighbors

In the movie *Avatar*, all the plant life in the forest is connected. Magical underground connections link the plants and trees in an interdependent whole. In nature, something just as magical can occur with some mycoheterotrophic orchids that form a tripartite relationship linking orchids, fungi, and trees. Ian Hood (2005) describes the unusual relationship between leafless *Gastrodia* orchids, five species of *Armillaria* fungi, and pine trees. Since planting pine plantations in New Zealand, large numbers of *Gastrodia* orchid tubers have been found surrounding the pine trees, infected with the fungi. The fungi coat the roots of the pine trees and absorb nutrients which they shuttle to the orchids. It is possible that the planting of pine plantations fostered the spread of the native orchids by enticing fungi into the area.

Another amazing tripartite relationship exists with the bizarre *Rhizanthella gardneri* orchid in Australia. *Rhizanthella gardneri* is a unique botanical oddity, an orchid that lives almost completely under the ground and enjoys a free ride, producing no food of its own—ever. Difficult to find and extremely rare, the orchid has no aboveground presence except for the small hole broken in the soil by the apices of the flower bracts. With a flower spike the size and shape of a small tulip, the waxy white and purple bracts of the flower protect a cluster of up to 120 maroon orchid flowers. Blind termites, attracted by the musky odor, and fungus gnats are thought to pollinate this subterranean beauty, the only known case of orchid pollination by termites. The distinctive odor of its berry-like fruit attracts marsupials which eat and disperse the seeds. This dispersion is uniquely different from the wind dispersal of most orchids' dust-like seeds.

This unusual species, *Rhizanthella gardneri*, was discovered in 1928 in the parched wheat belt of western Australia, where unsuspecting farmer John Trott dug

up the first specimen while clearing his land of broom honey myrtle trees (*Melaleuca ucinata*). When news of this weird, new orchid reached the public, there was great excitement in Australia and England. A wax model was paraded through England by the Royal Botanical Society. The orchids grow in nutrient-poor soil in a unique tripartite relationship with the myrtle tree and fungi. The myrtle tree, the host plant, grows densely around the orchid and provides all necessary sugars and nutrients to the orchid through a network of fungal threads that connect the two. The orchid does not need to produce any aboveground structures for photosynthesis.

Leafless, the orchid lives off other life forms in this amazing ménage a trois. The botanist for whom the orchid was named, Charles Gardner, noted that the first orchids were found near decayed stumps of the trees. He wrote that the "stumps and roots were partially rotten through the action of a fungus, the mycelium of which formed dense masses of a violet color and webby texture in the subsoil." (Rogers, 1980)

Living in such a specialized arrangement means that these orchids are vulnerable to environmental changes. Surveys since 2000 show that the myrtle tree is limited to handkerchief-size reserves due to salt encroachment and drought. Three of the known populations of *Rhi. gardneri* are protected, and conservation initiatives have been quite vigorous. A partnership between the Millennium Seed Bank of the Royal Botanical Gardens Kew, Australia's Endangered Species Program, and Kings Park Western Australia undertook DNA fingerprinting and seed-banking of the orchid and the myrtle tree. As of 2004, there were 123 plants of the orchid growing in the botanic gardens at Kings Park from seeds harvested from the last remaining specimens of the species. In 2004, they were growing so well that they were bursting out of their plastic pots.

In 1932, a worker at an alum mine north of Sydney found a second underground species, *Rhizanthella slateri.* Rarer even than *Rhi. gardneri*, it was not sighted again until 2002 when a 13-year-old boy, Evan Currall, found eight heads of the plant while bushwalking near the town of Buladelah. He said it looked like "a beautiful jewel." Two more species of *Rhizanthella* have been found as well, and some think that the genus may not be extremely rare, just rarely found.

Sexual Deception in Terrestrial Orchids

Fully one-third of all orchid species are liars and cheats. More than 85% of deceptive plant species worldwide are orchids, offering a reward decoy and not the real McCoy. They promise a pollinator a reward and deliver nothing. Worldwide, it is estimated that at least 38 genera of orchids are involved with food deception, and at least 18 genera practice sexual deception. This is particularly common among terrestrial orchids. In Australia, MOST terrestrial orchid genera are deceptive. They have some of the most elaborate pollination

Gastrodia sesamoides

strategies, an unfortunate fact that makes them vulnerable to extinction.

At least nine genera of terrestrial orchids in Australia practice sex deception, convincing male insects who are so aroused by the scent, look, and feel of an orchid that they try to mate with it. Called "pseudocopulation," or fake copulation, it is only fake for the poor insect. It is, however, real for the orchid. The insect doesn't score, but the orchid does. During the insect's frustrating amorous attempts, pollinia are picked up and delivered, and orchid sex is completed.

In Australia, the Caladeniineae, which includes the ten species of *Drakaea* or Hammer Orchids, rely on a subfamily of parasitic wasps called Thynninae, a mostly Australian group within the family Thynnidae, whose females lay their eggs into beetle larvae. Males are good fliers, but females don't have wings and spend their whole lives underground eating native scarab

Drakaea glyptodon

Chiloglottis trapeziformis

beetle grubs. The lip of orchids like *Drakaea glyptodon* looks like the wingless female wasp, *Zapilothynnus trilobatus.* For four days of her life, the real female wasp climbs out of the ground onto a shrub and emits her pheromone love call from glands in her head. Competition for females is intense, and a desperate male, catching her enticing fragrance, pounces on her, lifts her into the air, copulating in mid-air, and regurgitating food he has collected into her mouth. He leaves her after this honeymoon on the shrub where he found her, and she uses that food for the eggs she will lay underground.

The *Drakaea* species have evolved a scent that supposedly mimics the receptive female wasp. The unsuspecting male, trying to lift his dummy female into the air for the nuptial flight, is tilted forward onto the column by a see-saw-like hinge on the lip and comes in contact with the pollinia. Although there is some visual recreation of the female—the species has a maroon, glossy flower color and lots of warty protuberances, but the fragrance is the main attractant. Botanist Warren Stoutamire described how thynnine wasp males followed his car and came in through an open window to locate the drakaea he had placed out of sight on the back seat floor.

Sadly, having a very specialized pollination system puts *Drakaea* species at risk. First, the female wasp relies on eating beetle grubs, which in turn require root systems of particular native plants as substrate. A different species of thynnine wasp pollinates each species of the Drakaea species, and each produces a slightly different fragrance, making the orchid very reliant on a particular species of wasp. These ecologically linked components make the orchids very vulnerable to local extinction. If any of these are lost, there is only a limited scope for ecological substitution. As a result, five Hammer Orchid species out of the nine that exist are considered critically endangered, and one, *Drakaea andrewsiae,* is considered extinct.

A fascinating case of scent mimicry occurs with the Australian genus *Chiloglottis*, whose 26 species are all pollinated using basically the same wasp strategy. For example, *Chiloglottis trapeziformis* attracts its wasp pollinator, *Neozeleboria cryptoides,* with a unique compound, chiloglottone. The only other living thing that produces this unique molecule is the wasp, with females emitting this compound as a sex pheromone. This chemical, applied to the head of a pin, is sufficient to attract excited

male wasps that attempt to copulate with the pin head. Male wasps only do this with this one species of orchid and do not visit orchids that do not match this pheromone.

Many species in the European genus *Ophrys (*which means "eyebrow" because its flowers often have hairs like a female bee) also use sex deception. This strategy partly relies on the fact that the male bee pollinators emerge two weeks earlier than the females, the female will only mate once, and there are twice as many males as females. This temporary excess of males causes a low threshold of stimulation, and desperate, aroused males will mate with things that only vaguely resemble females. When the real females arrive, it usually reduces the visits to flowers that mimic females, although not always.

As a rule, odor is the long-distance attractant with the *Ophrys* species, but the short-range visual and tactile clues orient the bee for copulation. Many species have common names that reflect their visual resemblance to insects like *Oph. sphegodes (*the Early Spider Orchid), *Oph. insectifera* (the Fly Orchid), and *Oph. apifer*a (the Bee Orchid). Usually, the sepals and petals are colored, and the petals smaller, sometimes triangular or rectangular. The lip has no spur and is often velvety. The lip sometimes has a shiny blue mirror look that mimics the female's folded wings, and there can be an appendage on the apex of the lip that can be mistaken for the female abdomen. Some have a hairy margin to the lip that resembles hairs on the female bee, and others have two eyelike knobs at the lip base, with the

Ophrys sphegodes

Ophrys apifera

Ophrys insectifera

Ophrys bombyliflora

Cypripedium fargesii

column forming a basal stigmatic cavity. The ridge on the lip of *Oph. bombyliflora* (the Bumblebee Orchid) even resembles the ridge around the genitals of a female bee.

Orchids Imitating Fungi

Sex deception is not the only trick terrestrial orchids play on their pollinators. Some trick pollinators by looking like fungi, which the pollinator either eats or uses to lay its eggs. *Cypripedium fargesii*, a critically endangered species endemic to southwestern China, attracts its flat-footed fly pollinator by producing low-growing leaves that mimic fungus-damaged plant tissue. 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. The orchid leaves mimic fungus-infected plant tissue to attract flies that feed on liquid exudates of plants infected with Cladosporium mold that produces black mold spots. The fly thinks it is going to get a rotting leaf meal. Instead, they get nothing but a chance to pollinate the orchid. There are approximately five closely related species *Cypripedium* species in China that deploy this same strategy.

There are also strange orchids that look like mushrooms and smell like them. Fungus gnats lay their eggs in mushrooms, and the Australian *Corybas diemenicus* looks and smells like the fruiting bodies (mushrooms) of basidiomycete fungi. A group of these orchids resembles a patch of mushrooms growing in the leaf litter of the forest floor, enticing the pollinator to visit. While laying their eggs, the fungus gnats inadvertently pollinate the orchid tricksters.

Thelymitra and Food Fraud

Not all terrestrial cheats use sex deception or fungal imitation. Four out of five orchids that practice deceit to get pollinated are food mimics. For example, *Anacamptis israelitica* mimics the visual display of *Bellevalia flexuosa* (a member of the hyacinth family) and manages to fool its pollinator into visiting it even though it offers no food rewards. In Western Australia, beautiful blue *Thelymitra crinita* and *Thel. macrophylla* are thought to mimic blue *Orthrosanthus laxus* (a member of the iris family) that grows in the same area. One of the orchids, *Thel. macrophylla* produces a similar fragrance to *Orthrosanthus laxus*, but it is 30 times stronger than the model species, providing a super stimulus to its naïve bee pollinators. They are all pollinated by female bees that collect pollen from various flowers. Even their crumbly pollinia are similar. Fraudulent food mimics frequently employ visual deception that is very effective at a short distance. At least half of the 100 species of *Thelymitra* in Australia, the center of diversity for this genus, have blue flowers. The area is also rich in unrelated blue angiosperm flowers, making visual deceit much easier.

Most orchid flowers, once open, stay open. *Thelymitra* are unusual because they regularly open and close their flowers in response to the appearance and disappearance of sunlight. It has been suggested that this behavior may protect them from pollen-eating insects and that they open when the daily peaks of foraging are over; however, no one knows for sure.

Bellevalia flexuosa

Thelymitra crinita

Thelymitra macrophylla

Cypripedium calceolus

Cypripedium reginae

Cypripedium calceolus: The Lady's Slipper Orchid Suffers from its Beauty

Some terrestrial orchids are just too beautiful for their own good, and selfish admirers have wiped out many cypripedium (Lady's slipper) orchid populations worldwide. One of the problems of living in the ground is that it makes it easy for people to collect pretty orchids, even to the point of extinction. In Lancaster, England, the beautiful native *Cypripedium calceolus* was over-collected to the point that the last remaining British plant was cordoned off and guarded by hourly police patrols and surveillance cameras. Fiercely guarded, they say the orchid has a log number on the police computer! It is sad when these orchids are taken from the wild since their demanding fungal growth requirements so often condemn them to a speedy demise in cultivation.

The Sainsbury Orchid Conservation Project of the Royal Botanic Gardens, Kew, has been working for many years with the English Nature Species Recovery Program and others in raising these plants for reestablishment. The orchids are found in a single, fragile natural site, and hand pollination is carried out to ensure seed set. Some of the resulting seed is sent to the Sainsbury Orchid Conservation Project for seed storage and *in vitro* germination for growth and reintroduction. Cryopreservation seems to have the potential for long-term seed storage. The seeds are easy to store but difficult to germinate, and more study of this orchid's endophytes is ongoing. Unlike epiphytic orchids, the often-unique mycorrhizal association of many terrestrial species frequently results in limited success in propagation and translocation programs. Luckily, the species decline resulted from overcollection, and the habitat was little changed, so reintroduction is possible with a 75% survival rate.

The first six seedlings from seed collected from the native parent were planted in the wild and 1989, and the first flowered in the summer of 2000, eleven years later. In 2003, over 1500 seedlings were planted at 16 different locations. However, the small seedlings were vulnerable to slugs, snails, voles, and rabbits.

Cypripedium reginae: Minnesota's State Flower

Cypripedium reginae, the Showy Lady's Slipper, is perhaps the most beautiful of the state's 49 native orchid species. The name *reginae* means "queen," and this really is the queen of lady slippers. This gorgeous orchid, pink and white with a distinctive pouch, is Minnesota's state flower. Well-established plants can produce clumps with numerous flowering stems from one to three feet (91cm) high, carrying one to two and rarely three or four flowers. *Cypripedium reginae* is widely found throughout northern and eastern North America in shady bog margins, wet meadows, wet prairies, and cool, damp woods. Slow-growing, plants are only as tall as a pencil point the first year, taking 16 years before they bloom. From then on, they don't flower every year, most producing seeds only four or five times in their very long lives of more than 50 years. Once they do bloom, they can produce a half million dust-like seeds a year, making up for their slow growth.

A century ago, *Cypripedium reginae* frequently decorated church altars. Now the orchid is uncommon in Minnesota, hurt by wetland drainage, road construction, tree cuttings, uproots, and roadside herbicide use. In part of its range, it is prey to heavy deer browsing with plants consumed before the seeds mature. States were invited to establish a floral emblem to celebrate the 1893 Chicago World's Fair. Minnesota, the first to step up, chose *Cypripedium calceolus.* To their embarrassment, they later found out that the orchid did not grow in Minnesota, and they quickly changed the state flower to *Cyp. reginae*, which, thankfully, does grow there. Since 1925, the state has regulated the collection and commercial sale of the species, and now it is illegal to pick or uproot the flowers. In 1990, Governor Rudy Perpich declared 81 miles of Highway 11 a Minnesota Wildflower Route in honor of the hundreds of thousands of orchids that can be seen from the road. Minnesotans are so proud of their orchid that in Minneapolis, it even appears on manhole covers designed by Kate Burke.

Cypripedium acaule

Cypripedium acaule

Cypripedium acaule is the floral emblem of Prince Edward Island in Canada and the state flower of New Hampshire. Ranging from Georgia and Alabama to Newfoundland and the Northwest Territories, the orchid most often thrives with conifers in moist wooded areas. The species epithet *acaule* means "without a stem," a reference to the fact that the two hairy basal leaves rise directly from the underground rhizome. The flower stalk is not considered part of the stem, and the species is also called the Stemless Lady's Slipper or the Moccasin Flower.

The flower stalk has a single gorgeous, pleated, vermillion-pink flower (although 25% of the plants in New Hampshire are green with a white pouch) with an unusually small opening in the front of its large, inflated pouch-like lip. Although the flower gives little or no nectar, bees are attracted to the brilliant color, muscle their way into the opening in the front, and cannot force their way out. Trapped within, they are forced to exit another way, brushing past the stigma and affecting pollination.

A plant may go years between flowering, and only ten percent of plants may flower in an area in any one year. Interestingly, blooming increases after a fire, and it is thought that the fire opens the canopy, allowing in more light.

Its beauty has been its undoing and *Cyp. acaule* has been over-collected and commercially exploited. This is a great pity since its special relationship with fungi in the soil makes transplantation success very low. Rare and endangered, it is protected by law in Canada and parts of the United States. As far back as 1927, Herman Pepoon in *Flora of Chicago* noted that college students and florists would gather *Cyp. reginae* and *Cyp. acaule* in Illinois by the hundreds and then destroy the colonies to prevent others from competing with them. Pepoon observed a teacher taking out a carload of over 800 freshly picked orchids to sell to local florists. Now, there are only limited populations of cypripediums in these areas.

Zeuxine strateumatica

Orchids that Live in Disturbed Places Often Self-Pollinate

Terrestrial orchid species can readily establish colonies in disturbed places or unlikely new habitats. They are sometimes so successful that they are regarded as weeds. Blown in by the wind or carried on the muddy feet of birds, they pop up in unexpected places. Sometimes, they make the trip without their pollinator, and they cleverly develop an autogamous or self-pollinating strategy to survive and carry on.

In Hawaii, out of the three native, endemic (found nowhere else in the world) orchids, two self-pollinate. Only 3% of orchids self pollinate, so to have have 66% self-pollinate is of interest. Three of the four most common, naturalized (introduced by people) orchids in Hawaii can cross-pollinate and also reproduce asexually. Five out of seven of the endemic and introduced orchids have alternative means of reproduction, improving survival. Self- pollination is of short-term advantage because, of course, some pollination is better than extinction. Over the long term, cross pollination provides more variety than self pollination is therefore of more benefit long term.

Zeuxine strateumatica is one alien, weedy, terrestrial orchid that self-pollinates. It pops up so often in people's lawns that it is now disparagingly called the "Lawn Orchid" and is considered a nuisance weed. Originally native to Asia, this species is rapidly expanding its range throughout many parts of the globe. In Florida, first

Epidendrum nocturnum

Eulophia maculata

discovered in 1936, its seeds are believed to have arrived in a shipment of centipede grass from China that was used as turf grass. It is widespread across much of Asia and is rapidly naturalizing worldwide in places like Saudi Arabia, Brazil, northeastern Mexico, the West Indies, Hawaii, California, and the southeastern United States from Texas to Georgia. This rapid growth has occurred in the United States in only 70 years. A sturdy plant, it grows well in lawns, floodplains, forests, meadows, and even the cracks in sidewalks. It is often found in orchid collections, having arisen spontaneously, in pots and baskets of showier orchids. Many hobbyists unknowingly throw them out, unaware they are orchids, too!

Zeuxine strateumatica, about 10 inches (25 cm) tall, has a pointy spike of tiny flowers with glistening white sepals and petals and a golden spade-shaped lip. Though small flies will visit the flowers, this species is thought to mainly self-pollinate. It quickly flowers and sets seeds; one plant can easily result in hundreds and sometimes thousands of seedlings. After setting seed, the mother plant dies; however, these will often bud off new plantlets from their roots. Large stands will appear for one year but then remain dormant underground and not appear again for many years.

South Florida has been invaded by many alien orchids from places like South America, Africa, and Southeast Asia. Many orchids now considered native came from the New World Tropics and persist because they have established colonies of self-fertilizing plants to compensate for the paucity of native pollinators. Two tropical American species in Florida, *Epidendrum nocturnum* and *Bletia purpurea,* have developed cleistogamous (closed) flowers that fertilize themselves without the flower ever opening.

One of the most interesting Florida "aliens" is *Eulophia* (syn. *Oeceoclades) maculata*, which originated in Africa and has spread rapidly since 1980 in the New World. The attractive flowers are pink with a white lip blotched in bright pink. It blooms during Florida's rainy season and is self-pollinated with the help of raindrops. The weight of the raindrops falling on the flowers knocks the pollinia from the anther. Each pollinium is attached to a threadlike stipe that dries and curves down and back, pushing the pollinium onto the flower's stigmatic surface. This successful strategy produces many fat green capsules in late autumn or winter.

Eulophia maculata was once regarded as Florida's public enemy number one because of its rapid spread. It was placed in the highest category of the Florida Exotic (meaning foreign) Pest Plant Council's list of most invasive non-native plants. It still is ruthlessly ripped out and destroyed by public land managers even though it has now been removed from the state's list of invasive non-native species. Hawaii has placed several naturalized orchids on its Hawaii Pacific Weed Risk Assessment and has identified *Arundina graminifolia, Spathoglottis plicata,* and *Vanda tricolor* as invasive weeds. It is

Arundina graminifolia

Epipactis helleborine

hard for orchid hobbyists to IMAGINE an orchid that is undesirable!

Many other self-pollinating orchids have flown the coop and made a home outside their native territory. *Epipactis helleborine c*an be found in lawns, construction sites, and mine tailings in Europe (where it is native) and North America; *Spiranthes cernua* pops up in sand pits and ditches in North America; *Microtis media* is found in temperate southern Australia and *Disa bracteata* in temperate Australia. Opportunistic tropical and subtropical terrestrial orchids include *Arundina graminifolia* from roadside clearings in Malaysia and Hawaii and *Spiranthes hongkongensis* from roadside slopes in Hong Kong.

So here we have a formula for terrestrial orchid success outside its native range—vegetative propagation, self-pollination, copious seed production, and rapid growth.

Caladenia: Taking Nutrition by the Collar

Caladenia, a genus of more than 250 species in the subtribe Caladeniinae of the Tribe Diurideae, is endemic to Australasia. This weird and wonderful group includes terrestrial orchids that spends a good part of their lives underground as geophytes. They can remain dormant for even a year or two, nourished only by their fungal partners. Named from the Greek "calos" or beautiful and "aden" or gland, the ornately structured calli on the lip give each flower a distinctively unusual appearance. This group includes some of the most conspicuous of Australasia's 900 taxa of geophytic orchids.

The growth habit of caladenias is most amazing and unusual. With various pollination mechanisms from selfing, food and sexual deception, and actual rewards, they rapidly set seed capsules that mature in four to six weeks. Like all orchids, calandenia require the intercession of mycorrhizal fungi through hairs or trichomes to develop to the protocorm stage.

After six to twelve weeks, calandenia's distinctive growth form consists of a single, often erect, hairy leaf arising from a deeply buried underground tuber and often large, colorful, or complex flowers. Most species occur in dryland habitats, mainly from the temperate southern region of Australia, although several are found in wet places like swamp margins. In fact. *Caladenia cristata* and *Calda. paludosa* from western Australia spend part of the growing season with their lone leaves fully submerged and their flowers perched just above the water line of waterlogged soils and swamps.

Caldenias endure a summer dry season dormancy, with growth at the end of the summer initiated by increased moisture and a temperature drop. A shoot from the tuber grows to the surface and produces a single green leaf with a swollen area called the "collar," just below the soil and leaf litter surface. This structure, unique to the Caladeniinae, is the point of entry for the

Caladenia latifolia

Corybas diemenicus

mycorrhizal fungi through trichomal hairs that will support the plant during its dormancy.

This collar, right in the leaf litter, gives the orchid a competitive and nutritive advantage over orchids that rely only on their roots for fungal penetration. However, the collar makes the orchid vulnerable to the harmful effects of drought and changed fire regimes that are common in Australia. These effects cause the loss of organic material from the surface and physical disturbance to the ground.

Caladenia has more species under threat than any other Australian orchid genus, comprising five percent of threatened flora, one-third of critically endangered, and forty percent of endangered species. Of particular concern are species with a specific fungal preference and a very specific pollination strategy. For example, *Caladenia latifolia* can tolerate a wide range of fungi and provides a generalized food deception based on bright colors and a sweet fragrance. We would expect this species to be less threatened than a species like *Caladenia huegelii,* which requires a highly specific fungal partner and uses sex deception through a single wasp species for pollination.

Orchids on the Mantle

Specialized strategies of some terrestrial orchids allow them to survive in the most inhospitable of places. *Corybas sulcatus* and *Corybas dienemus*, the Grooved Helmet Orchid and the Windswept Orchid, survive on the exposed crest of the mostly undersea Macquarie Ridge, halfway between Australia and the Antarctic continent. It is the only place on the planet where rocks from the earth's mantle, usually 4 miles or more beneath the surface, are exposed, raised to their present position when the Indo-Australian tectonic plate met the Pacific plate. It is a place of very strong winds, stormy seas, and earthquakes in a treeless land. Penguins, seals, albatrosses, and elephant seals endure the freezing and harsh conditions on this small speck in the Southern Ocean.

These two endemic corybas grow low to the ground, clinging to whatever warmth the earth provides. Critically endangered, they were probably introduced on the muddy feet of birds. They spread easily, even with a paucity of pollinators. The orchids are capable of autogamy (self-pollination) and strong vegetative reproduction. During self-pollination, the pollinia break up and fall on the stigma, a handy strategy when pollinators are scarce. Both species are deciduous, replacing leaves, stems, and underground root tubers annually.

Catasetum fimbriatum

It most commonly reproduces through the production of daughter root-tubers on lateral underground elongate stolons or stems and forms extensive colonies. Vegetative reproduction is a common strategy for orchids with absent or infrequent pollinators and is, in the short run, very effective at prolonging species' survival. Interestingly, birds eat the roots for food, leaving broken fleshy roots and root tubers on the ground after feeding. Amazingly, new plants can grow from these broken stolons, stems, or displaced root tubers, which could be why these species are so widespread in this place.

Twin Tubers: Hot Salep and Frozen Viagra

The name "orchid" means testicle since several terrestrial orchid genera, like *Orchis* and *Ophrys,* have twin tubers, one larger than the other. One is used for this year's growth and the other for storing material for next year's growth. Tubers are not roots but are the swollen underground stems of plants used for storage. Many terrestrial species are deciduous and survive the dry season by growing a subterranean fleshy storage tuber, some reaching the size of a small potato. In 50 AD, the Greek writer Dioscorides wrote an early medical text called "The Doctrine of Signature." He claimed that if something looked like a body part, it must be good for treating that body part. Because of the resemblance of these orchid tubers to testicles, they were used for thousands of years in attempts to cure venereal disease, promote fertility, increase male performance, and help with childbirth. Today they are still being consumed to promote virility.

Salep, a popular drink served hot or cold in Turkey and throughout the Middle East, is made from dried and ground orchid tubers mixed with sugar, milk, or cream. The name "salep" comes from the Arabic "sahlab" and the Hebrew "sakhlav" and means "fox's testicles," a graphic description based on the shape of the orchid tubers. In London, there is a Saloop Street where people used to sell hot salep with breakfast before introducing coffee and tea. An even more popular Turkish ice cream, "dondurma," is made from salep tubers, comes in 32 flavors, is eaten with a knife and fork, and is so elastic you can jump rope with it. Men line up around the block for this ice cream, thought to be a kind of frozen Viagra. The drink is still popular in Turkey, and I watched a television show which showed people drinking salep hot with sugar and cinnamon. Unfortunately, the fascination with this aphrodisiac results in the decimation of the tuberous orchids in Turkey. Just one ice cream manufacturer will kill 12 million orchids a year, threatening them with extinction.

In the Central African country of Zambia, tuberous orchids are made into a loaf with ground peanuts that is very popular in sandwiches and as a snack in high-class restaurants. It is driving genera like *Disa, Satyrium,* and *Habenaria* to extinction in neighboring Tanzania.

The Differences Between Epiphytic and Terrestrial Orchid Roots

There are significant differences between epiphytic, lithophytic, and terrestrial orchid roots. Epiphytic and lithophytic orchid roots are exposed to air and light and are photosynthetic, perennial, and fairly constant throughout the year. On the other hand, the roots of terrestrial orchids are non-photosynthetic, live less than three years, and often show seasonal differences in growth and composition. They are usually buried in soil or leaf litter, unlike the aerial roots of epiphytes. Moreover, terrestrial orchids depend much more on fungi living on or in their roots than epiphytic orchids. The velamen layers of tropical epiphytic orchids are often thicker, attached to bark, and exposed to drying. Tropical orchids like *Catasetum fimbriatum* or *Stanhopea lietz*ei can have 15 layers of velamen to absorb water rapidly. Temperate orchids, more often terrestrials and living in moist dirt or humus, don't require a thick velamen.

Mycotrophic orchid roots, with their alternate food source, seem nutritionally independent of the rest of the plant. The fascinating consequence is that detached root fragments, remaining alive in the soil for a long time, can sometimes give rise to new plants. For exam-

ple, if a short, infected side root of *Cephalanthera rubra* is detached, it can live and produce a bud that forms a new rhizome and can produce leaves. Similarly, when the rhizome of a species of *Neottia* dies, many mycotrophic roots are released, each capable of independently producing new plantlets from the root tips. Interestingly, both of these genera have mycoheterotrophic and photosynthetic members.

Living in the Dirt

As we have seen, terrestrial orchids have made the best of living in the ground. They utilize the abundant soil fungi as a critical food source. They have learned to doze in the dirt when conditions are not right for their growth. They have developed mechanisms to attract pollinators, having even learned to fool them into doing their bidding, or self-pollinate. Terrestrial orchids have truly learned to make the best of the place where they grow.✾

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About the Author

Carol Siegel, a retired English teacher, and medical office 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. She has written articles on Nevada's native orchids in addition to many wonderful articles for the *Orchid Digest*. Carol was awarded the *Orchid Digest* Medal for her meritorious service to orchids.

E-mail: growlove@cox.net