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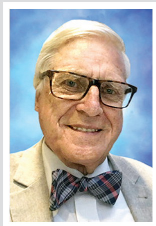
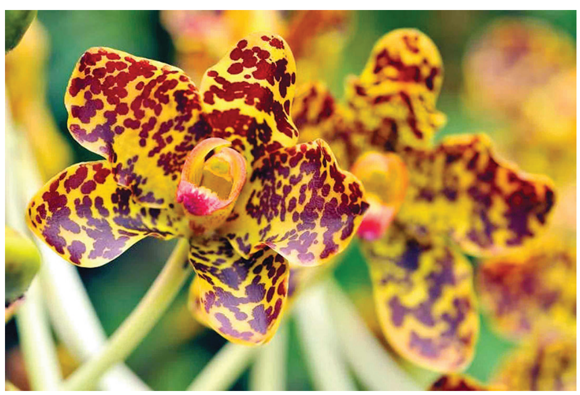


CRITICAL FOCUS

Brian J. Ford

Aliens of the Botanical World

Orchids have long been important to microscopists. The cell nucleus was first identified in orchids, and some species are so minute they require a microscope to be clearly observed.



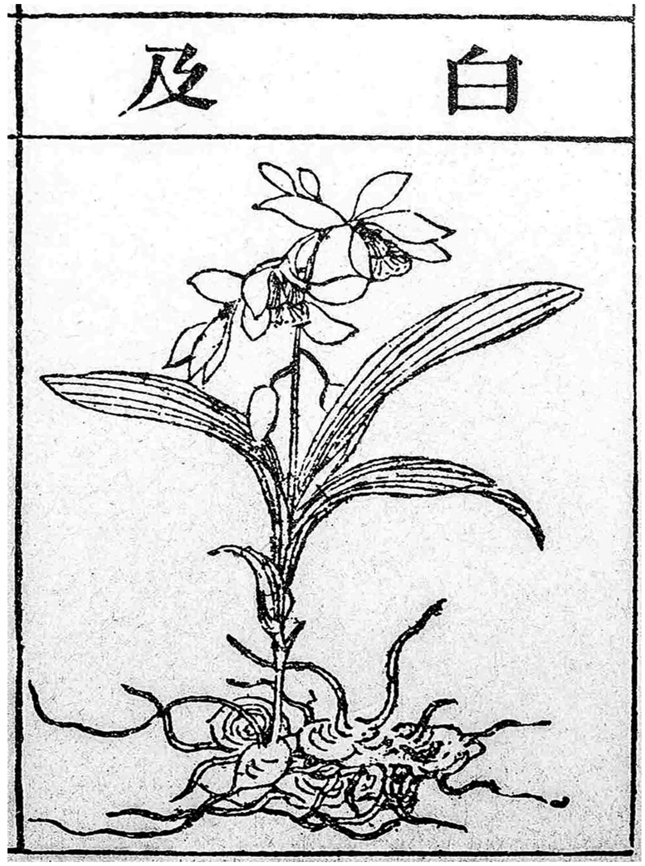
The tiger orchid, *Grammatophyllum speciosum*, is the world's largest orchid and produces plants weighing more than a ton, with blooms 4 in. (10 cm) across. A 2-ton plant was shown at the Crystal Palace exhibition in London in 1851, and a specimen collected in Penang, Malaysia was exhibited at the Columbian Exhibition in Chicago of 1893.

We were hiking up the tallest mountain in Borneo when I saw it. Nestling on a rain-wet branch was the tiny but unmistakable flower of the Pinhead Orchid, *Podochilus tenuis.* The local botanists knew it well; it had been studied since its discovery in 1833 and measured some 2 mm (8/100 in.) across — the smallest known orchid in the world. Others have since made similar claims. When *Platystele jungermannioides* was recently discovered in Ecuador, it was no smaller, though was immediately claimed as the record holder. Then *Campylocentrum insulare* was spotted in Brazil during 2015, looking like a tiny fungus and recognizable as an orchid only under the microscope. In Australia you will find *Bulbophyllum minutissimum* less than 1.5 mm (6/100 in.) — and all these diminutive flowers have petals that are only one cell thick. These are the smallest land plants anywhere on earth.

We usually think of orchids as normal-sized plants, and something so minuscule is counterintuitive. Yet there are orchids that are among the biggest of all flowers. *Paphiopedilum sanderianum,* discovered in 1886 in Malaysia, has petals that grow 90 cm (3 ft) long on stalks measuring 2 m (over 6 ft). In the rain forest where we saw the Pinhead Orchid there are plants of *Grammatophyllum speciosum* weighing several tons and measuring a good 7 m (20 ft) in width.

Orchids are astonishing, and they are related to the light microscope in so many ways. Many of the tenets of basic botany are ignored by the orchids. They're like aliens. Yet 10% of all flowering plants are orchids, and they are the largest family of all angiosperms, with around 30,000 species. Many are epiphytes and their green roots need sunlight to survive; others grow as lithophytes on rocky strata with very little organic soil. They occupy almost every ecological niche, from sea-spray covered cliffs

Amateur naturalists Jean and Fred Hort photographed this specimen of *Rhizanthella gardneri* in Western Australia. These parasitic orchids live on the roots of broom plants, and though they can be exposed to the air, they live their entire lives underground. It is assumed that termites and other insects pollinate the blooms.



Traditional Chinese medicine has long involved orchids for therapy. This woodcut shows *Bletilla,* traditionally used to treat bleeding and is currently under investigation as a hemostatic agent. It appeared in *Bencao Gangmu*, compiled by herbalist and naturalist Li Shizhen in 1578 and published in 1596.

to tropical rainforest, from arid desert landscapes to snow-covered polar rocks, and from open prairie to cold, wet woodland. Very few places (St. Helena, Tristan de Cunha) are too isolated for orchids to have reached, and some (Nauru and the Marshall Islands) are too new for orchids to have colonized. Yet they haven't conquered every niche. Although they often abound in marshes and swamps, not a single orchid is aquatic.

The most unconventional habitat is that of *Rhizanthella gardneri,* first discovered in Western Australia. It is entirely subterranean. This bizarre orchid was found by a farmer, John Trott, in 1928, who plowed up fleshy rhizomes in an area of broom bushes, where no corresponding leaves were visible above ground. He sent specimens to the Western Australian Herbarium, where the botanists realized they were orchid plants, and they were named after Charles Gardner, the botanist who conducted the research. Then in 1931, a collector in New South Wales found the same subterranean rhizomes intertwined with the roots of plants he was collecting, so the underground orchid was known from both east and west Australia. Lacking chlorophyll, they are parasitic on plants of *Bromus*, the broom, and they even flower underground. Nothing is known of how they are pollinated, though they are unique in having seeds like ball-bearings. These subterranean orchids are threatened with extinction, though we still have much to learn about their amazing life cycle.

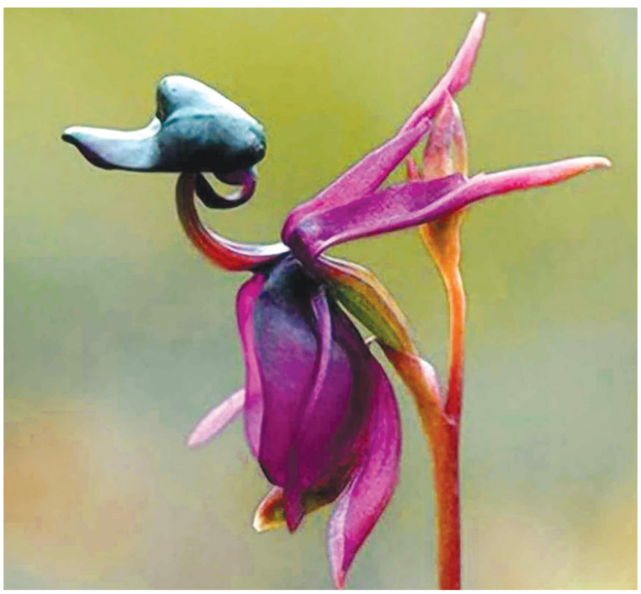
Although we think of orchids as tropical, exotic and alluring, they are commoner than people think. I knew of wild orchids as a child and surprised my parents by pointing them out in the spring as they flourished among the grass in wild meadows. Orchids are found in the unlikeliest of places. The Northern Marsh Orchid *Dactylorhiza purpurella* grows wild across Europe and Scandinavia, extending up into artic Norway and across Russia. It is even found in Alaska. The Small Round-Leaved orchid *Galearis rotundifolia* flourishes in Greenland. Others have restricted distribution. *Ophrys lesbis* grows only on a few Greek islands around Lesbos, while the rare Ghost Orchid *Dendrophylax lindenii* is restricted to a few cypress swamps in Cuba and Florida. Hochstetter's Butterfly Orchid *Platanthera azorica* was first identified by a German botanist, Karl Hochstetter in 1838 on an island in the Azores, a tiny archipelago perched in the middle of the Atlantic. He recorded it in meticulous detail, and it was so rare that botanists who subsequently scoured the islands never saw another specimen — until one was discovered on the island of São Jorge in 2011. Another was found on the nearby island of Faial in 2017. That's rare.

We know orchids through their flowers. All share the same anatomy, with three petals growing in a whorl and three sepals. The central petal is enlarged, and this lab ellum is colored to attract pollinators. Some orchid blooms last for only a few hours, as in the genus *Flickingeria*. The flowers of *Sobralia* survive only for one day, so the plants ensure pollination by gregarious. These plants are extremely sensitive to climatic change, and — when a specific temperature is reached — all the plants in the area bloom spectacularly at the same time. Other genera have flowers that survive for weeks, and the blossoms of *Grammatophyllum speciosum* remain open for nine months. The internal structure of the orchid reproductive system under the dissecting microscope is unique. Rather than anatomically diverse male anthers and a female stigma, as in a conventional flower, most orchids have both male and female reproductive organs retained within a unique tube-like structure at the base of the flower, the gynostemium. The pollen is not available for liberal dispersal, but is produced as coherent clumps called pollinia. An adhesive pad (the viscidium) can stick the pollen mass to a visiting insect, enabling cross pollination to occur. *Cycnoches,* the swan orchid, is one of those rare genera that is dioecious, male and female plants being separate. The tropical genus *Catasetum* even displays sexual dimorphism, with male and female flowers being so anatomically distinct you would never imagine they were the same species.

Exquisite lithographs of orchids appeared in *L'Illustration Horticole*, a periodical magazine published in Ghent, Belgium, from 1853 to 1896. This compelling study of *Houlletia chrysantha* was published in 1871. It shows the floral structure vividly and (bottom right) illustrates the pollinia under a dissecting microscope.

Many orchids are pollinated by flies, bees, butterflies, and moths. In some species, insects are attracted by nectar or by scent from the blooms, and simply carry adhesive pollinia from one flower to the next. Others are more highly specialized and use subterfuge to achieve their ends. In the Central American rain forests you can find the bucket orchids of the genus *Coryanthes.* The labellum of each flower is shaped like a scoop, and the plant secretes sweet, syrupy nectar that attracts euglossine bees. The surface of the labellum is actually slippery, so a visiting bee is likely to lose its footing as it attempts to sip the enticing nectar, and falls into the bucket. Many insectivorous plants obtain their nutriment from drowned insects, but the bucket orchid is more ingenious by far. *Coryanthes* has evolved to allow the trapped bee to escape. At the rear of the bloom is an opening through which the near-drowned bee manages to extricate itself, and — as it climbs out into the fresh air — the pollinia are firmly glued to its back.

Several orchid genera are known as the Bee Orchid, but *Apis apifera* is the European species and the best known. It attracts male bees eager to abandon their virginity in an act of copulation that is doomed to fail, but which the orchid exploits to attach its pollinia to the visiting insect's thorax.



The flying duck orchid *Caleana major* has an extraordinary resemblance to a drake. Other orchid blossoms look like bees, birds, and monkeys. *Dendrophylax lindenii* from Florida has the appearance of a ghostly miniature frog. Such beautiful and bizarre forms are hard to reconcile with conventional evolutionary theory.

BIRDS AND THE BEES

My favorite orchid as a youngster was *Ophrys apifera*, the bee orchid. It looks like a bee, and this genus can produce allomones, chemical complexes whose odor can influence the behavior of animals. *Ophrys* flowers can seduce male bees into attempted copulation, thus collecting (and transferring) pollen. This has sometimes been described as cooperation between plant and insect, but it's actually the exploitation by the plant of an insect's lust for sex. All the textbooks explain how the appearance of the flower evolved to attract those hapless bee pollinators, though it's hard to discern the evolutionary mechanism (I have discussed this in *Autonomy of the Living Cell, Driving Force of Evolution*, "The Cell as Secret Agent — Autonomy and Intelligence of the Living Cell: Driving Force of Development," *Academia Biology*, https://doi.org/10.20935/AcadBiol6132). Some species of *Ophrys* look just like a female bee, her head buried in the deep recesses of the flower, her wings outspread; the unwitting male bee will alight and perform vigorous movements of copulation, only to remain sexually frustrated because — for all the appeal of the morphology — the anatomy doesn't fit. Instead, his enthusiastic attempts to mate ensure that the pollinia become firmly stuck to his back, so he eventually flies away bearing what look like bright yellow water wings. He looks like an insect scuba diver with yellow air tanks ready for action.

So perplexed is this male bee that he doesn't think to try again for a while. His energies have been spent. He won't try again until he is recovered, and he is likely miles away by this time. So he will either mate with a female bee, or he may be fooled again by an orchid, in which case the pollinia are deposited adjacent to the reproductive organs, and pollination is achieved. It's an excellent example of the mimicry and ingenuity that abounds in nature.

The Australian genus of tongue orchids *Cryptostylis* takes matters a stage further. These strange blooms attract male wasps and lure them into full copulation, including ejaculation of spermatozoa. So agitated does the insect become that they are soon covered with glue-like secretions from the viscidia and become smothered with pollen, in prime position for transfer to the stigma of another bloom when the wasp has recovered. Other orchids have adaptations that are less subtle. *Bulbophyllum* and *Porroglossum* have petals that are hinged and close over an insect, forcing its back against the pollinia so they become firmly attached. The South American genus *Catasetum* goes one better: there is a trigger within the bloom which, when touched by an insect, causes the pollinia to be shot firmly against the insect, securing them to its thorax.

Also in South America we find *Trichoceros antennifer*, which produces blooms that mimic female flies of the genus *Paragymnomma*. The petals and sepals are marked with yellow and brown stripes and two extend to look like the wings of a sitting female. The column and base of the lip are narrow, barred with yellow and red-brown, and they extend laterally to simulate the extended wings of a sitting insect. The males are attracted to the stigma of the flowers, which has the appearance of the sex organs of a female fly and, as they land, the flower's viscidium becomes firmly attached to the male fly's abdomen. The Australian orchids of the genus *Cryptostylis* have evolved to be pollinated by *Lissopimpla* ichneumon wasps. The male wasp bends its body into an arch, as it does in copulation, and is forced to press itself against the sticky pollinaria. There seems to be no end to the range of remarkable mechanisms orchids have evolved to ensure that pollination ensues.

So many insects are attracted by pollen, and many bees possess sacs on their legs, which they pack with pollen grains while foraging. Pollinia are not attractive to such creatures, of course, so some orchids produce imitation pollen intended to attract pollinators. This pseudopollen sometimes consists of pollen-like papillae, or it may form from detached epidermal hairs filled with starch and evolved to look like clumps of powdery pollen. These orchids, of the genera *Maxillaria* and *Polystachya*, attract bees to their apparent rich deposits of pollen, and then glue the actual pollinaria to the insect while it fumbles around, gathering what it believes to be pollen.

You might think that flowers would evolve to use multiple means to transfer pollen from one bloom to the next. In many angiosperms that's true, though orchids are a law unto themselves. Pollinators are usually species-specific. The Christmas star orchid *Angraecum sesquipedale* from Madagascar produces sweet-smelling nectar at the base of an elongated spur. Charles Darwin studied this striking flower and noted its 10-inch-long (25 cm) spur. He concluded that the pollinator would be discovered to be a moth with a correspondingly lengthy proboscis. He was correct. The only insect in the orchid's habitat with a tongue long enough to reach the prize is the hawkmoth *Xanthopan morganii* and this turned out to be the sole pollinator of the orchid.

Many orchids have developed to be pollinated exclusively by birds, and have bright colors to attract birds, typically yellow, red, or purple. Insects do not detect colors towards the red end of the spectrum, though these are the wavelengths that are attractive to birds. Their flowers all form a tubular structure to which small birds are attracted, where a strategically placed callus forces the bird against the pollinia so it will transfer pollen to the next flower they visit. The bird-pollinated orchids tend to produce pollinia that are brown or gray, rather than yellow. These colors match those of the bird's beak, so they are less likely

How could evolutionary theory lead to the emergence of the remarkable White Egret Orchid *Pecteilis radiata*? The resemblance to a bird in flight is unmistakable, but the similarity can confer no benefit to the orchid, which has no means of aspiring to mimic its conspicuous counterpart.

to be noticed and wiped off before the bird has visited the next blossom on its route and has safely delivered its cargo of pollen.

About 1,000 orchid species rely exclusively on hummingbirds to do the task. Contrary to what many believe, hummingbirds do not feed exclusively on nectar. The nectar provides the carbohydrate source they need to maintain their energetic flight mode, but a quarter of their daily dietary intake is in the form of insects, which provide the proteinaceous nourishment. Hummingbirds pick insects from flowers or open their beaks like swallows and dart forward to catch flies on the wing. Orchids provide a plentiful supply of nectar for hummingbirds, and the anatomy of the bird's tongue is uniquely adapted to collect it. Under the microscope it can be seen to be bifurcated, the lobes of the tongue being incurved to form a tube. Nectar is drawn into the tube — likely by capillary action — and then expelled into the mouth as the tongue is repeatedly thrust forward and back during feeding. The exposed surface of the tongue may be fringed, which serves both to collect additional nectar and also to trap insects.

Hummingbirds are found only in the Americas, and the bills of northern and southern species are morphologically distinct. The tropical species of the south have variously shaped curved bills that are matched with the shape of the flowers on which they feed. There is no cold season, so there is always an abundance of blossoms available in the tropics, and morphological adaptations are an advantage. The hummingbirds found in North America have straight bills that can be used to collect nectar from a range of different flowers. There are pronounced seasons, and the range of flowers from which they will have to feed is vast, so a general-purpose beak is more functional. Some of the delicate bills of hummingbirds develop rows of fine teeth, which seem to be used in combat over territories or would-be mates.

Perhaps the most remarkable example of an orchid pollinator is the white-bellied rat *Rattus fulvescens*, which pollinates *Cymbidium serratum*, an orchid from China. The blossoms produce an odor that attracts the rats, and they then feed on the orchid's succulent labella. As they do so they acquire the orchid's pollinia, firmly stuck to their fur, and transfer the pollen therein next time they go to consume another blossom. No other group of plants boasts such a diverse range of pollinators.

Orchids are the weirdest flowering plants in the world. Although one that looks like a bee seems to have a certain evolutionary logic lurking behind it, how would you explain one that mimics a monkey? *Dracula simia* has a blossom that looks uncannily like a miniature monkey. A native of Ecuador, this curious plant is in danger of extinction in the wild. Then we have *Pecteilis* (or *Habenaria*) *radiata*, the white egret orchid, which looks uncannily like an egret in flight. And what of *Caleana major*, the flying duck orchid from Australia? Its resemblance to a drake is bizarre. Clearly, there is no mimicry in these remarkable plants.

The range of orchid colors is greater than in any other angiosperm family, and the introduction of interspecific hybridization extended the possibilities ad infinitum. The first artificially produced orchid hybrid was produced in 1858 by a gardener named John Dominy, who worked for the Scottish-born Victorian horticulturist John Veitch. The Veitch nurseries boasted a range of hothouses in Exeter, in the temperate southwest of England, which became the largest exotic nursery in the whole of Europe for a century. Veitch had a remarkable penchant for growing exotic plants, and Dominy succeeded in creating a hybrid between *Calanthe masuca* and *C. triplicata.* It was named *Calanthe Dominyi* and is available from garden centers to this day. These two species come from China and Japan and are closely related. Hybrids occur spontaneously among plants growing in the wild.

In 1889, Veitch announced that his first new orchid had bloomed. This was a cross between the greenish *Cymbidium iowianum* and *Cymbidium eburneum*, with ivory white flowers and a pink-spotted labellum. Nobody had managed to do that before. Its distant descendant gave rise to the first black orchid, *Cymbidium* Kiwi Midnight. This is hybrid originated with *Cymbidium iowianum,* discovered and named by Heinrich Gustav Reichenbach in 1879. His father Ludwig Reichenbach, founder of the Dresden botanical gardens, had published the authoritative *Icones Florae Germanicae et Helveticae* in 1849, and Heinrich became the greatest orchid specialist in Germany. Large and showy plants of *C. iowianum* are found growing as an epiphyte on trees (and sometimes on damp rocky outcrops) in the rain forests of China, Thailand, Myanmar, and Vietnam. The flower is a yellowish green with maroon markings on the labellum, and this plant — vernacular name Low's boat orchid — was awarded the Award of Garden Merit by the Royal Horticultural Society of London.

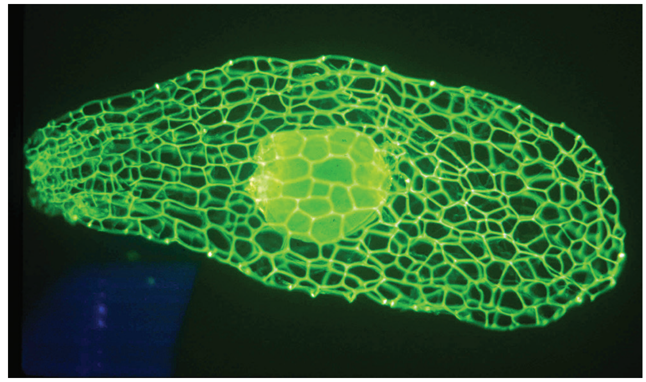
By the turn of the 20th century orchid enthusiasts everywhere had caught onto this curious craze, so new orchid varieties and novel hybrids were soon appearing everywhere. In 1915, Sir George Holford crossed Veitch's *C. iowianum* with *C. sanderae* to produce the interspecific hybrid he called Garnet. This was crossed with *C. iowio-grandiflorum* by Holford in 1923 to produce a hybrid named Bustard (that's not a typographical error; a bustard is a bird). In 1935, the Bustard orchid was crossed with a hybrid named President Wilson by botanists Armstrong and Brown in the English town of Tunbridge Wells to give us the Chiron hybrid, and in 1942, that was crossed with Lysander to give us Doris Aurea, originated by Black & Flory of Whitstable (on the north coast of Kent, the center of English oyster production). By 1989, Geyserland in New Zealand had crossed Doris Aurea with Doctor Baker to produce Janet Holland, yet still none of these was dark in color. Doctor Baker is red, while Doris Aurea is pale pink, and the hybrid still featured the spotted labellum of the original *C. eburneum*. Hybridizing orchids calls for dexterity and diligence, but there's no way of knowing what the results might be. Then, in 2001, a New Zealand orchid enthusiast crossed Janet Holland with the purple Khairpour hybrid, and the seeds germinated to give the spectacularly dark flowers of Kiwi Midnight. The black orchid had arrived.

HOW BLACK?

Black orchids have long been the subject of legend. Several novels have Black Orchid as the title, and it's the name of a series of books by DC Comics. The first movie with that title was a silent film from 1917; there have been several others since, including one with Ronald Howard and another with Sophia Loren. Several songs are entitled Black Orchid, and there used to be a famous nightclub of that name in Chicago. That's the good news; the bad news is that the Kiwi Midnight orchid isn't actually black, but a very dark velvety purple. That's not as disappointing as *Prosthechea cochleata*, the Black Orchid of Belize, which has it as their national flower. It has nothing black about it, and features a pale yellow blossom with a fringe of purple. This strange little flower is of interest to botanists because the labellum forms a protective hood; it grows upside down.

A recently released perfume is named Black Orchid, by Tom Ford (no relation, as far as I know). A bottle of 100 ml will cost over $100. Other perfumes have been inspired by orchids, from "Nuit d'Orchidee" by Yves Rocher and Calgon's Tahitian Orchid to the O Boticário company's Orquídea Noire and several Orchid perfumes from Zara. This is because orchids are known to produce a bewildering range of scents, though I am not certain whether any plant extracts are incorporated into the recipes for the perfume products. Most perfumes are made from odiferous chemicals. I smile when I pass those stores selling bath bombs and potpourris. Customers are convinced they're being treated to bags of dried petals from strongly scented blooms, or packs of bath additives soaked in essential oils from powerfully scented flowers. It all seems so enticingly natural — but it isn't. The aromas are from blends of compounds like ethyl butyrate, methyl propionate, or geranyl acetate, often blended with powerfully scented essential oils. And the term "essential" oil is ambiguous, though people don't realize the fact. The term is taken to suggest that the oil is something essential, but it isn't: the "essential" in this context means that it conveys the essence of the plant. Garlic oil, for example, provides the essence of garlic. That's why it is an essential oil — but that doesn't mean that it's essential you have some!

The scent of an orchid is produced by glands known as osmophores, which variously secrete terpenoids, aromatics, and aldehydes. Confusingly, the term osmophore is separately used to connote the chemical groups that produce the scents, as well as the scent-glands themselves. The range of odors is extraordinary. The Lady of the Night orchid *Brassavola nodosa* smells strongly of lily of the valley, while *Rhynchostylis gigantea* has a powerful citrus aroma, and *Encyclia alata* emits the scent of coconut. By contrast, *Liparis* flowers are a greenish color and have a disgusting aroma, like stagnant pond water. They are pollinated by fungus gnats that thrive around stagnant waterweeds. Worst of all, orchid odors are those of *Bulbophyllum beccarii*, which smells like decaying



Wilhelm Barthlott reveals the remarkable simplicity of a minuscule *Limodorum abortivum* orchid seed using fluorescence microscopy to display the cell walls. The embryo is the denser portion at the center. Barthlott includes other examples in his co-authored book *Orchid Seed Diversity*, published in Berlin, 2014.

flesh, and *B. echinolabium*, which is like dog droppings (like the legendary durian fruit of Southeast Asia). The arthropods that consume those items in the environment are drawn in to pollinate the orchid.

The best-known olfactory experience from the orchid world is one that most people would not associate with orchids, but with ice cream: vanilla. This widely popular flavoring is extracted mostly from the flat-leaved orchid *Vanilla planifolia*, sometimes from the Tahiti vanilla orchid *V. tahitensis*, and rarely from the West Indian vanilla *V. pompona.* These plants are vines, with thick fleshy stems scrambling among woody vegetation and often grow to 100 ft (about 30 m) from root to tip. The flowers are pale green or yellow and are pollinated by bats. They produce elongated fruit capsules, which are popularly known from their shape as pods. These pods taste of nothing. There is no vanilla flavor in a fresh vanilla pod. It is just as I explained in the case of cacao, which has no chocolate flavor when freshly harvested ("Beer and Pizza: A Slice of Ancient Life," *The Microscope,* 64:4, pp 173–185, 2016). The characteristic taste of vanilla is produced by fermentation by bacilli, most commonly *Bacillus subtilis.* This spore-forming, harmless soil bacterium is ubiquitous and is widely cultured to produce enzymes on an industrial scale. When vanilla pods are spread out and dried in tropical heat, these bacteria proliferate and release the characteristic taste and aroma of vanilla.

The fermentation process takes months, and the end result is about 1% pure vanillin in the pods. Vanillin is 4-hydroxy-3-methoxybenzaldehyde, and it can be synthesized on an industrial scale so it is widely used in catering and food production. Ice cream is sometimes marketed with vanilla seeds visible as tiny dark specks scattered through the product, though the seeds are not always genuine — there are plenty of other dark particles that can inexpensively substitute for the real thing — and in any event, the seeds aren't important, for they are flavorless. The most convenient way to use vanilla flavors is to keep a handful of the dried pods in a tall jar of sugar, which will absorb the intense, appealing flavor. Using the vanilla sugar in recipes confers just the taste you want on your dishes. The pods do not need to be replenished until the taste starts to fade.

Vanilla flavors are not new. The Olmec people of Central America were using it 3,000 years ago, and it was famously farmed over 1,000 years ago by the Totonac people, who still inhabit the eastern coast of the Gulf of Mexico. Totonac uses for vanilla included as incense in temples, to ward of disease in amulets, and also for flavoring their food. When the Aztecs invaded and settled much of the Totonac lands in 1427, they used vanilla to temper the bitter taste of their cocoa beverages, calling the concoction "xocolatl."

Although the meso-American people knew how to pollinate and propagate *Vanilla planifolia* plants, it was not until 1837 that the Belgian botanist Charles François Antoine Morren found a way to pollinate cultivated plants. His process proved to be too difficult and unreliable for commercial use until 1841, when a 12-year-old slave on the island of Réunion in the Indian Ocean, Edmond Albius, discovered a quick and easy way to do it.

Most of the vanilla used in the West is industrially produced, though this does not impart the same flavor as the real thing. The natural fermentation of the vanilla pods, as well as vanillin, also produces large numbers of other biochemical compounds, including acetaldehyde, acetic acid, furfural, eugenol, methyl cinnamate, hexanoic acid, and 4-hydroxybenzaldehyde. Each, though present in small amounts, imparts a taste of its own.

SEEDS SO SMALL

Almost all orchid seeds are microscopic, less than a millimeter long. The Swiss philosopher and naturalist Conrad Gessner drew the ovaries of orchids, the seed capsules, and the dust-like seeds in his studies during the 1540s. Jeremy Bock, a German botanist known formally as Hieronymus Tragus, wrote of orchids a decade later, insisting that they arose from bird semen by a process of fermentation. Bock did dissect the seed pods of orchids but wrote that they contained nothing but fine dust. He could not accept that this dust could be the seeds, and not until the investigations of his compatriot Georgius Everhardus Rumphius, around 1660, did the truth emerge. He described the seeds as being like flour or sand; the dust others had observed was, after all, the seeds of orchids.

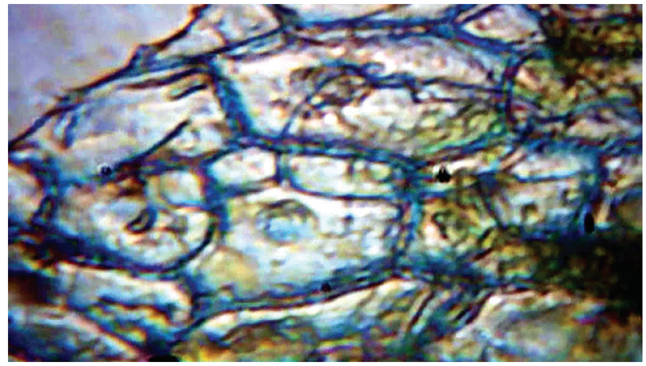
Orchid seeds are the smallest in the world. So small are they that there is no room for any food storage organs, so an endosperm rarely develops. There are a few microscopic oil droplets within the cells, as an energy reserve, but that's not enough to fuel the emergence of a new plant. The smallest of all are the seeds of *Aerides odorata*, native to Southeast Asia, which are smaller than many free-living microbes and measure just 200 µm. A single seed capsule of the Central American orchid *Cycnoches chlorochilon* contains some 4 million seeds, an astonishingly high number that far exceeds any other family of flowering plants. The inconceivably large number of seeds orchids release is necessary because of their simple structure. They will not survive alone; they need to find a fungus partner. Hardly any do.

The only exceptions are a few species of *Disa* from South Africa, which have evolved to survive without external help, but every other orchid depends for their essential carbohydrate supply on a mycorrhizal association with specific microscopic fungi. If the fungus isn't present, the seeds cannot survive. The germinating orchid seed develops into a protocorm, a minute structure unique to orchids, which not only attracts the mycorrhizal fungus but also modifies the way the fungus grows. Hyphae of the typical mycelium penetrate the cells of the orchid protocorm and are induced to change their method of growth. They form a curious looped structure known as a peloton, which is harnessed by the orchid cell for its own benefit. The orchid extracts all the nutriments it needs from the growing peleton by diffusion, and later — as the peleton matures and breaks down — by absorbing what remains. It is as though the microscopic fungus sets out to parasitize the host plant, only to be commandeered by the orchid and used as its vital source of nutriment during the earliest stages of germination. How such complex interrelationships could have evolved is beyond our comprehension.

The proteins needed for life are nitrogenous compounds, and you do not find those growing on a tree. The leafless epiphytic orchids colonizing a branch (occasionally growing on rock) must derive all their nitrogen from the atmosphere. We all know legumes as the plants to fix nitrogen, and they are a family unique in their possession of root nodules within which grow bacteria like *Rhizobium*, which can draw in gaseous nitrogen and convert it to soluble nitrate. Most is in the form of ammonia that the host plant can absorb ("Coming Up for Air," *The Microscope,* 69:3, pp 123–134, 2022). Many orchids have cracked it too. Not all — this is not a property of the entire family, like the Leguminosae[1] — but the incredible ingenuity of the orchids has allowed many of them to harness their own communities of microbes to do the job for them. We rarely hear about that.

Like other epiphytic species, the leafless orchids have green, photosynthetic roots. A team at M. V. Lomonosov Moscow State University, Moscow, led by Elena A. Tsavkelova, have just unveiled what lies within. Not only did they utilize phylogenetic analysis, they also brought in denaturing gradient gel electrophoresis. Most important, they embarked on systematic microscopy to reveal what was happening in these complex communities, and the results are astounding. Roll over *Rhizobium*, the Moscow team have discovered entire communities of blue-green algae fixing nitrogen for the ultimate benefit of the host plant. Three families of filamentous cyanobacteria were observed, in the Oscillatoriales, Synechococcales, and Nostocales. The composition of the cyanobacterial community varied, depending on the nitrogen supply. Two of the most important genera are *Leptolyngbya* and *Komarekiella,* relatives of the familiar *Nostoc*. The proportion of each species varies with the prevailing conditions. These cyanobacteria are widespread in nature, and we can only wonder how often they perform nitrogen-fixation for higher plants. These discoveries will open our eyes to entire new areas of microscopical research, all spearheaded by the incredible lives that orchids live.

Most of the orchids people grow in their homes are epiphytes, accustomed to living in the branches of tropical trees, where they do not rely on soil for nutriment or for their supply of moisture. Indeed, the genus *Epidendrum* is from the Greek and literally means "upon tree." These orchids absorb the moisture they need from the humidity of the air, through a tissue coating of the roots called velamen. I am not sure how it works, and nobody else seems to be sure, either. Most sources agree that velamen is composed of dead cells (they look dead when sectioned and mounted under the microscope) and are largely devoid of contents. But



Robert Brown named the nucleus from his studies of orchids. For years his single-lens microscope was dismissed by scientists as a low-power dissecting 'scope not up to the task. I took this micrograph of epidermal cells of *Cymbidium* with Brown's lens magnifying 170×. The cell nucleus can be clearly observed.

many orchids have velamen that is clearly alive; the cells in these examples are rich in cytoplasm and often show mycorrhizal associations or communities of bacteria that probably fix nitrogen and provide accessible ammonium compounds for the root cells within.

You would think of orchids the moment velamen is mentioned, though it's not unique to that family. Many of the Araceae develop velamen, often in several layers, so does *Agapanthus*. We once had *Monstera deliciosa*, the Swiss cheese plant that thrives so well indoors, growing profusely in the bathroom. It had numerous adventitious roots hanging down and covered with velamen. A young dog decided to sample it and chewed through the main stem at the base. The plant wasn't bothered but carried on growing as if nothing had happened. It was absorbing all the water it needed from the steamy atmosphere — through its velamen layer. The standard texts all say that velamen protects the roots, shielding them from the sun's harmful rays, and helping to absorb water. Velamen acts as a sponge, though I wonder how it attracts so much moisture. Someone should research velamen; it can give these plants all the water they need, largely by drawing it out of the air. That's a neat trick, and we need to know how it's done.

A common complaint about growing orchids at home is that they fail because the roots die, and they often say it's due to over-watering of the compost in which they've been potted. But it isn't the water that's the problem, it's the compost. These epiphytes should never be planted in compost at all. That's not where they have evolved to live. They would rather be in a tree, high in the forest canopy, with their curious layer of velamen gathering what they need from the

[1]The familiar family Leguminosae has been renamed the Fabaceae, a term nobody likes and hardly uses. It was decided, by a botanical committee far, far away, that all plant families must contain a representative genus from which the family must take its name. No, they don't — there is no such requirement. It's as sensible as Elon Musk changing Twitter to X.

air rather than from soil. Epiphytic orchids should be planted in a translucent plastic pot, firmly bedded in a coarse granular medium like volcanic pebbles, broken bark, or osmunda fiber; grow them in perlite, sphagnum moss or fir bark. These epiphytes are unlike any other plants. Their roots demand light and air, and the last thing they want is being buried in soil. I have experimented with water-retaining granules scattered among the growth medium. They hold large amounts of water, that will be slowly released to maintain the kind of humidity the roots would find in a rainforest, while being transparent and so allowing plenty of the light they need to pass. These carbohydrate polymer gels can absorb 500 times their weight in water and release it over time. I think this may provide the clue to growing orchids effortlessly at home.

Charles Darwin was a consummate observational naturalist, yet he was perplexed by orchids and strove to have the seeds germinate. He failed in his attempts and wrote that he had a "passion" for orchids and derived "great pleasure to fancy that I shall see radicles of orchid seed…" but this was not to be. The first tiny root of a germinating seed, the radicle, is typical of flowering plants as the seeds germinate, but it doesn't occur in orchids. The protocorm develops instead, and there isn't any sign of a tiny rootlet. If Darwin had tried to germinate his orchid seeds on a bed populated by the necessary fungi, he would have observed this unique stage in the lifecycle; but mycorrhizal associations were not to be discovered until 1885, when a plant pathologist named Albert Bernhard Frank realized that some of the fungi he observed under the microscope in infected plants were there to help, not hinder. Without their fungal commensal, those orchid seeds do nothing.

THE NUCLEUS REVEALED

Orchids had, meanwhile, bequeathed to us one of the fundamental concepts in modern biology, the cell nucleus. Robert Brown was a Scottish botanist and military surgeon who used his single-lensed microscope to study the intricacies of fertilization in plants. His observations were remarkably detailed, all the more so when we consider the simple nature of the instruments he had at his disposal ("Charles Darwin and Robert Brown — Their Microscopes and the Microscopic Image," *Infocus*, 15, pp 18–28; https://doi.org/10.22443/rms.inf.1.48). In 1831, he was studying orchid tissues under the microscope, when his attention was caught by something that Antony van Leeuwenhoek had noted some 250 years earlier: a rounded body in the middle of the cells he was watching so intently. Leeuwenhoek had been studying the blood of salmon and cod. The red cells (erythrocytes) of fish are different from those of mammals, in that they contain a nucleus. Leeuwenhoek noticed this feature and wrote about it in 1682: "It seemed to me that some of them enclosed in a small space a little round body or globule," he said. By 1804, the Austrian microscopist Franz Bauer had noted a central body within the cells of plant tissues, and in 1831, Brown observed them in orchid epidermis under his microscope. It fell to Robert Brown to give them their name: "In each cell of the epidermis of a great part of this family, a single circular areola is observable…. This areola, or nucleus of the cell as perhaps it might be termed, is not confined to the epidermis." And there we have it. Brown came close to paraphrasing what Leeuwenhoek had written one and a half centuries before him, and by giving it a name, his term "nucleus" became one of the most fundamental concepts in modern medicine and cell biology.

The ancestral evolutionary line of orchids began to emerge in the middle of the Cretaceous period. Eustatic sea levels were high, the weather was warm, and the globe was largely covered with shallow seas and lakes. After my aquatic dinosaur theories were published in 2012, my late colleague Bill Hay of the University of Colorado — widely regarded as the world's greatest paleoclimatologist — realized that the conventional concept of the Cretaceous landscape needed radical revision. I had proposed that, prior to the tectonic upheaval that gave rise to our familiar continental masses, paleoelevations were far lower than today, and the land surface was largely covered with water. Hay and his co-workers looked again at their data, on the basis that up to three-quarters of the world had been covered with water (lakes, seas, wide meandering rivers, and swamps). This new view of the land also revolutionized our understanding of the atmosphere. It was already accepted that levels of carbon dioxide were five times greater than today, at 2,000 parts per million. But my proposal that the world was mostly covered with water led to the conclusion that the resultant raised levels of water vapor in the air exerted an additional greenhouse effect. That was why we observed a warm, humid, wet world in the Cretaceous. It was perfect to provide buoyancy support for our gigantic dinosaurs, and the endless warmth and high levels of CO_2 created the ideal climate for the development of an astonishing array of newly emergent plant families ("Aquatic Dinosaurs Under the Lens," *The Microscope*, 60:3, pp 123–131, 2012). My theory proposes that plate tectonics caused the demise of the dinosaurs, rather than a climatic apocalypse caused by that asteroid. Plant life would have been exterminated by an enduring winter; but they lived on, and from those early angiosperms the orchids were to emerge.

We have no fossil records of orchid flowers going back so far. Those prehistoric plants grew in hot, tropical forests where the moist conditions meant that dead orchid plants or dropped blooms disappeared within weeks. They would have rapidly rotted away, leaving no traces to become fossils. However, in 2007, a team at Harvard published an account of Miocene amber containing a perfectly preserved bee with unmistakable orchid pollinia attached to its back. They gave the orchid its new name, *Meliorchis caribea*. The specimen came from Dominica and dates back some 20 million years old. By applying cladistic analysis, they calculate the date of the first orchid-like flower around 80 million years ago.

Surprising as it seems, orchids are not the delicate, tropical, exotic plants that we like to think. The world's greatest authority on orchids is my greatly respected friend Joe Arditti, Emeritus Professor at Irvine, whose insights illuminate the subjects we discuss like a flashlight in a cinema. Years ago I had been given a showy *Phalaenopsis*, which proudly flowered until its season was done, and was then discarded in the garden (being overseas so often, it never made sense to cultivate houseplants that would need regular attention). It stood outside, neglected and ignored for an entire winter. Next spring? Several leaves suddenly sprouted, and within weeks a flowering head appeared and we were once more treated to a beautiful show of blossoms. When I told Joe, he smilingly remarked: "Orchids are tough plants." That took me by surprise, but it's clearly true. I purchased one for my wife last fall, hoping it would bloom through the holiday season. Its final flowers are dropping as I write, 10 months later. Yes, orchids are tough.

A WORLD OF ORCHIDS

Orchids are spectacular when grown en masse. The greatest orchid display in the U.S. is at the Huntingdon Botanical Gardens in San Marino, CA, which has over 10,000 orchid plants representing almost 4,000 unique varieties and covering over 1,500 species of 280 genera from *Paphiopedilum* and *Phragmipedium* to *Stanhopea* and *Lycaste*. Most of their greenhouses are for propagation and closed to the public, but there is always one spectacular display in their vast exhibition greenhouse. You can find almost 10,000 orchid plants at the Smithsonian. The Smithsonian Gardens opened 50 years ago with just five orchid plants; today they have 10,000. There are 7,000 representing almost 300 genera on display at the Missouri Botanical Garden; 6,000 orchid plants at the Marie Selby Botanical Gardens in Sarasota, FL; and some 2,500 at the Nani Mau Garden on the Big Island, Hawai'i. The Fuqua Orchid Center at the botanical garden in Atlanta opened only 20 years ago, but already shows 2,000 species of over 200 genera, and a range of spectacular hybrids.

Orchid hybridization has been perfected at the Singapore Botanic Garden, where the spectacular orchid garden is the largest display in the world. The garden's deputy director Yam Tim Wang (center) is presenting an example of current cross-breeding experiments with my experimental physicist colleague Lee Hock Cheong (right).

Around the world there are collections ranging from the Soroa Orchid Garden in Cuba to the orchid collection at the Gothenburg Botanical Garden in Sweden and the Ernest Thorpe Orchid House in South Africa. Many specialized centers put on displays; at Chicago Botanic Garden there is an Orchid Show of Wonders planned for Feb. 10–March 24, 2024, with an orchid Ferris wheel as the center of attraction. In South Africa, the Durban Botanic Gardens, of which the orchid collection is a highlight, were established in 1849 as a commercial outpost of London's Royal Botanic Gardens in Kew. And Kew has their own orchid display at the Princess of Wales Conservatory. No visit to London is complete without calling at Kew.

The greatest place to revel in the world of the orchid is Singapore. This independent state derives its name from the Hindu prince Sang Nila Utama from Sumatra, who saw a lion on the island during a hunting trip around the year 1290. He recorded it as *simhapura*, Sanskrit for lion city, and the lion is the symbol of the state to this day. It remained a swamp-covered jungle island until Sir Stamford Raffles landed there

Scientists at Singapore Botanic Garden named this hybrid of *Papilionanda* after Vice President Kamala Harris to commemorate her visit during the Covid-19 pandemic in 2021. The island state, once the biggest supplier of orchid hybrids, indulges in "orchid diplomacy" to celebrate ties with leading personalities from countries around the world.

from Sumatra on Jan. 29, 1819, and recognized it as a potential colonial outpost for the British Empire. Raffles drew up a town plan for development, and had a causeway constructed to connect the island to mainland Malaysia. By 1822 he had set up a Botanical and Experimental Garden on a hill near the center of the south coast. Raffles was a keen naturalist, and this was one of his first projects.

The Singapore Botanic Garden was set up by the Agri-Horticultural Society in 1859 and is a UNESCO World Heritage Site. Their work on orchids rapidly expanded, and on Oct. 20, 1995, Lee Kuan Yew opened the National Orchid Garden. Singapore is only 85 miles north of the equator, so the climate is perfect for growing and studying tropical orchids. Indeed, I've always been amused that many exotic plants grown in Singapore are in glasshouses that are specially cooled. The last thing they need is a hothouse.

I've no idea how many orchid plants grow there (and I doubt whether anyone could count them all), but the orchid garden is home to 1,200 species of orchid and some 2,000 hybrids. It's a breathtaking array of color and scent. Beautiful hybrids have become their hallmark. They created orchids named for Princess Diana, Queen Elizabeth, and Margaret Thatcher. There is a *Paravanda* Nelson Mandela, *Renantanda* Kofi Annan, and a purple-pink hybrid *Papilionanda* was named to honor a visit by Kamala Harris. This is part of Singapore's "orchid diplomacy" program, which began when Lady Anne Black (the wife of Sir Robert Black, a popular governor of Singapore) had a hybrid of *Aranthera* named after her in 1956.

There is, of course, a Raffles orchid. It's white. When I first lectured in Singapore on a world tour back in 1978, statues of Sir Stamford Raffles were regarded as legacies of an imperialist past. His bust at the Raffles Junior College had been relegated to a storeroom at the back of the building, and there were thoughts to throw it out. In the present century his legacy has been recognized, and the last time I spoke there, he was in the entrance hall, suitably garlanded with orchids.

Orchid research at Singapore leads the world. They have studied means of optimizing hybridization and became famous for exporting showy, colorful hybrids, though labor costs have reduced the output in recent years. They are now reintroducing native species back into the wild. Singapore was once home to a couple of hundred indigenous species, but the development of the island slashed that number to a handful. The number of extinct species has been officially catalogued as 152. However, these species flourish elsewhere in Southeast Asia and are being systematically reintroduced. Over 20,000 plants have been planted out in more than 40 different locations and so far, 33 native orchids are known to be re-established in the wild.

I have often visited the research laboratories in Singapore, though the first person I knew who cultivated orchids was an avuncular Irish physician, who lived in Newport, Wales when I was young. He had greenhouses filled with exotic-looking blooms. Botanists from Europe flew in to see them, and it seemed miraculous. In 1965, I booked him to appear in a program for the BBC. I had been invited to join the BBC many times, and always explained that — though I enjoyed broadcasting and thought it was a wonderful way to bring accessible science to a wider audience — I had no intention of giving up a life in science and becoming a full-time broadcaster. But I did make one historic change to the way they worked. I negotiated a way of producing programs independently and providing the finished article ready for them to transmit. The first of my independent BBC documentaries was called "The Gentle Dictators," and it looked at how scientists worked to benefit society. One of those in the mix was my physician colleague, explaining how he managed to coax orchids to grow into such luxuriant, prolific forests of flowering plants. It all seemed so surreal and remarkable back in the day. Now you can pick up orchids in the local supermarket or gas station for a few bucks. And my legacy at the BBC remains: now it's quite normal for them to commission outside production of their popular programs. Just sit back for half a century, and the wildly experimental becomes the everyday. Botany or broadcasting, it's all the same. ■