

ORCHID  
POLLINATION  
ECOLOGY



# Orchid Pollination

Exploring a Fascinating World

BY RON MCHATTON



[1] The first example of sexual deception in Australian orchids involved the genus *Cryptostylis*. These orchids are pollinated by male parasitic wasps of the genus *Lissopimpla*. Here four male *Lissopimpla excelsa* wasps compete for the favors of a *Cryptostylis erecta* flower.



[2] Silver-spotted skipper (*Epargyreus clarus*) pollinating a small purple fringed orchid (*Platanthera psycodes*) at Mt. Mitchell, North Carolina. The long spurs of the orchid have nectar at their ends and the skipper must push its proboscis deep into the spur to get to the nectar. Note the pollinia attached to the base of the skipper's proboscis.



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NO ONE IS REALLY SURE HOW LONG ago orchids evolved but recent fossil evidence suggests that the development of pollinia was well established at least 75 million years ago and perhaps earlier (Ramirez 2007). The development of fused reproductive structures, the so-called column, and pollinia are rare outside the Orchidaceae and set the stage for the development of an extremely varied and fascinating reproductive ecology. Pollinia, more-or-less fused, relatively large masses of compact pollen grains, because of their mass are not effectively distributed by water or wind and require the active intervention of an animal, typically an insect, to effect pollination. In addition to the dependence on a pollen vector, or pollinator, orchids have also evolved myriad pollination syndromes or mechanisms that run the gamut from advertisement and reward to sexual mimicry (Dressler 1981). Humans tend to think of the world in anthropomorphic terms and forget that orchid flowers have the shapes and fragrances they do not for us, but to ensure one thing and one thing only — successful reproduction.

**THE POLLINATORS** It has been estimated that about 60 percent of the orchid family is pollinated by wasps and bees (essentially pollen-collecting wasps) (van der Pijl and Dodson 1966). The form and symmetry of orchid flowers suggests that one of the first steps that separated orchids from their close relatives may have been the adaptation to pollination by this group of pollinators. Bee-pollinated flowers are often gullet flowers or modifications of this type of flower. In so-called gullet flowers the floral segments create a sort of chamber in which the pollinating insect must enter in the process of gathering pollen. In orchids, especially *Sobralia* and *Cattleya*, this chamber is often formed from the lip

[3–4] *Sobralia* [3] and *Cattleya* [4], two genera from very different parts of the orchid family, share parallel evolution of the gullet-flower structure characteristic of bee pollination. In these genera, the chamber is formed from the lip and column alone; the remainder of the flower serves as advertisement. Here they are illustrated by *Sobralia veitchii* and *Cattleya labiata*. Growers: [3] Bruce Rogers, [4] Fred Shull.

and column alone and the remainder of the flower functions only as advertisement. While perhaps harder to see, the flowers of *Stanhopea* species can be interpreted as gullet flowers since it's the "chamber" formed by the complex lip and column that controls pollination in these orchids. The remainder of the flower has evolved to tissue-thin texture and reflexes completely to effectively "get out of the way" of the action. Because the pollinating bee must first enter this chamber the bee does not receive or deposit pollen when it enters the flower but only as it leaves, thereby making self-pollination highly unlikely. In addition, many orchids prevent self-pollination by their pollinating vector by requiring a reorganization only occurring over some minutes as the soft tissues of the stipe dry and curl. Specificity of pollinator and pollinated species is achieved through adaptation of chamber size and column placement to insect size. Compaction of orchid pollen into pollinia with sticky structures makes pollen placement much more precise than that of most other flowers and a single bee species may serve as the pollinator of multiple orchid species without interference. As an example, *Dendrobium infundibulum* and *Cymbidium insigne* appear to use the same

bumblebee species. In this case, pollinia of *Den. infundibulum* are placed on the head of the bee while that from the *Cymbidium*, with much longer column, becomes attached to the bee's central thorax. Because the column of the former species is much shorter, only pollinia placed near the front of the bee will be in a position to contact the stigmatic surface of the *Dendrobium* column as the bee exits the flower (Du Puy and Cribb 2007).

Orchids with large gullet flowers such as *Cymbidium* are typically pollinated by large carpenter bees and bumblebees are known to pollinate *Spiranthes* and are implicated in the pollination of northern and some high-elevation species where other large bees are less common or active. Some bees gather oils from flowers rather than nectar or pollen and many orchids have evolved to attract these pollinators. A couple of examples include *Ornithocephalus* and some species of *Oncidium* that have elaiophores (open, nectar-producing glands) on the lateral lobes of the lip (Buchmann 1987). Orchids pollinated by bees and wasps also share a suite of characteristics in addition to the presence of some form of gulletlike or bowl-shaped floral structure. Bee- and wasp-pollinated orchids exhibit a wide color range with the exception of true red because bees and wasps cannot see red. Fragrance, if present, will be sweet or spicy and noticeable during the daylight hours when these pollinators are active. Bees and wasps land to gather pollen or nectar so the orchids they pollinate have well-developed landing platforms, nectar guides, either structural or visual and sturdy connection to the column to allow the bees to grasp the flowers. Rewards, offered nectar or food, may be real or perceived and may or may not be concealed in a nectary (what we orchidists typically think of as a spur); the latter is a common feature of orchids pollinated by nectar-feeding bees and the length of the nectary is directly related to proboscis (tongue) length in the pollinating species (Dressler 1987).

In addition to wasps and bees, orchids are pollinated by a whole range of creatures including, but not limited to euglossine bees (also called orchid bees), flies, butterflies and moths, as well as many species of birds; each pollinator group is attracted by a specific combination of attractants and forms. Euglossine bees, closely allied to bumblebees, are limited to tropical America. They range in size from about the size of a typical housefly to some large species. This group of bees is so closely involved in the pollination of many orchids that they are often called orchid bees. However, they



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are also involved in the pollination of many tropical American plant families. Females of some species pollinate nectar-producing orchids such as *Sobralia* and in that mode resemble other bee pollinators. However, it's the males of the species that are much more important in orchid pollination. Male euglossine bees collect fragrance oils from the surface of the flowers they visit and store them in specialized hollow pockets in their hind legs. These oils are then used to attract mates. Because fragrance is the key to attracting these bees, orchids pollinated by male euglossine bees have powerful, often resinous fragrances and will be fragrant during daylight hours. In addition, because nectar is unnecessary, these species do not produce nectar nor are nectar guides present in the floral structures. But wait you say, what about *Coryanthes* species. These plants are pollinated by male euglossine bees and they have unique liquid-producing glands that fill the characteristic bucket with fluid. These glands aren't nectar producing. Their sole presence appears to be to create a liquid reservoir that, once the pollinating bee enters by accident, leaves the bee unable to fly and the only escape route is out a narrow, dry passage past the column with its anther and stigmatic cavity.

While male euglossine bees land to collect fragrance oils, their mode of flight allows them to maneuver like helicopters and even land on vertical surfaces. As a result, orchids pollinated by such bees may or may not have well-developed landing platforms. Examples of euglossine bee pollinated orchids include all of the Catasetinae and Stanhopeinae as well as most members of the Zygopetalinae and some Oncidiinae. Pollinator specificity is maintained by either a specific euglossine bee-orchid interaction based on fragrance composition or, in the case of promiscuous bees, a specific size relationship. Such is the case with many species of *Stanhopea* which may be visited by many euglossine bee species. One species will fit correctly within the cavity formed by the lip epichile, mesochile horns and the ventral surface of the column, thereby properly aligning the



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pollinia with the opening of the stigmatic cavity. The specificity of chamber size to pollinating bee is so strong in the genus *Stanhopea* that two examples of the same species may have overall flower size that differ by as much as 50 percent while the column and lip cavity opening will be identical. Remember that the sepals and petals in this genus serve only to provide a protective covering during flower development and advertisement during anthesis.

The complex relationship between male and female euglossine bees and the plants they pollinate can be illustrated by the Brazil nut tree (*Bertholletia excelsa*). Plantation farming of this nut tree has proven difficult to do with reasonable yield because of this complex interplay. The tree

- [5] Pollinia of *Dendrobium infundibulum* on the head of a bee (left) while that from *Cymbidium insigne*, with much longer column, is attached to the bee's central thorax (right).
- [6] Male euglossine bees collecting chemicals from rotting wood. Note the enlarged hind legs used to store these chemicals and the orchid pollinia attached to the backs of two of the bees.
- [7] Male *Euglossa viridissima* visiting *Gongora powellii* in cultivation. These bees are known to visit other *Gongora* species in the wild.



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- [8–9] Orchids adapted to butterfly and moth pollination have noticeable spurs. The length of the spur is tightly tied to the proboscis length of the pollinating moth or butterfly. Long-tongued hawk moths pollinate species such as *Angraecum dollii* [8] characterized by a very long spur while *Aerangis citrata* [9] is pollinated by a moth with a much shorter tongue.
- [10] A sarcophagid (carrion) fly carrying pollinia from *Satyrium pumilum*, an African species that attracts its pollinator by mimicking the smell of carrion.
- [11–12] Fly pollinated orchids often are outfitted with hairs and other moveable parts that attract the attention of the pollinating fly. The tassellike ornamentation on *Bulbophyllum phalaenopsis* [11] and *Stelis villosa*<sup>1</sup> [12] appear to mimic maggots feeding on the flower. In the case of *Bulb. phalaenopsis* this ruse is further strengthened by the fragrance of the flower — carrion. Growers: [11] Bill Weaver, [12] Lynn O'Shaughnessy.

is pollinated by female long-tongued euglossine bees of the genus *Eulaema* (Mota Maues 2002). These bees are strong enough to lift the coiled hood on the nut tree flowers and possess a tongue long enough to snake its way through the complex, coiled flower to reach the nectar reserve. The presence of the female bees is dependent on the flowering of an orchid species that does not grow on the nut tree. The orchid flowering causes a swarming of the males of this bee species who are attracted to the orchid's resinous fragrance, collecting it to be used in attracting female bees. The swarming of the male bees causes the swarming of female bees that feed on, and pollinate the nut tree. Think of it as sort of the insect equivalent of a singles bar.

Butterflies and moths are nectar feeders and are almost as common pollinators as bees. Because of their long, coiled tongues, orchids adapted to butterfly and moth pollination have a narrow spur or nectary and belong to a floral classification called keyhole flowers. In many species, such as those of *Angraecum* and *Aerangis*, the spur may be pronounced. In many others, such as many species of *Epidendrum*, the nectary is

created from the fusion of the lip to the underside of the column and the only feature that may be visible is the keyhole formed between the underside of the column and the nectar guides or lip crests. Butterflies and moths are normally associated with pollination of flowers that have few ovules. This is because, in nonorchids, pollen is usually transported adhering to the insects' tongues and their long narrow tongues are not suited for carrying large quantities of pollen. Orchids avoid this problem because the pollinia become affixed to the insects' head, or in the case of *Tipularia discolor*, to the eye of the pollinating miller (Whigham and McWhety 1980). Butterflies and some moths (mostly those that are day-active), unlike bees, see red and many butterfly pollinated orchids are bright pink, red, yellow or even vivid violet.

Because visual clues appear to be the most important attractant for butterfly pollinated orchids, fragrance is usually lacking. Moths on the other hand, especially those that are nocturnal, can really only distinguish light from dark and a common characteristic of moth pollinated orchids is that they are white, cream-colored or green

<sup>1</sup>Formerly *Pleurothallis schiedei*.



and are typically fragrant, the aroma acting as an additional attractant in the darkness. Since nature wastes nothing, moth-pollinated orchids will exhibit fragrance only during the period of day or night in which the particular pollinator is active. As examples, *Tipularia discolor* is pollinated by a small Miller active only just before and after sunset and as a result this orchid species is fragrant for only a period of a couple of hours beginning about one hour before sunset. By contrast, *Angraecum sesquipedale* reaches its peak fragrance only during the wee hours of the night. Examples of orchids pollinated by butterflies and moths include *Brassavola* and many *Epidendrum* species as well as most of the Angraecinae and Aerangidinae. There are examples of specificity similar to those between male euglossine bee and orchid as well. For instance, *Epidendrum anceps* is visited by males of a single species of Ctenuchid moth and the species which comprise the *Epidendrum paniculatum* complex attract male Ithomiid butterflies (Adams and Goss 1976). Flies, including mosquitoes, represent a diverse group of insects and pollinate a wide range of orchids, including most

pleurothallids and many Bulbophyllinae. The floral features involved in attracting flies depend on the group of flies involved. In the case of mosquitoes, the insects function essentially as tiny moths and may take the place of moths at high latitudes. At least one orchid, *Platanthera obtusata* is known to be pollinated by mosquitoes (Thien and Utech 1976). A second group of prominent orchid-pollinating flies are those that collect oils. Orchids pollinated by oil-gathering flies are characterized by open- or shallowly-cupped flowers with disagreeable odors during the daylight hours. Orchids with fecal odors are pollinated by oil-collecting flies. In addition, because the fly is attracted to the appearance of excrement or something decomposing, most oil-gathering fly-pollinated orchids are either brown or red-purple. Nectar, in the form of the oil the flies collect, will always be present and many orchids so pollinated will have shiny wet structures visible on the flower as is the case with many *Bulbophyllum* species. Many flies, especially carrion flies, are attracted to fringes and it is thought that the movement associated with the fringes is sensed as either maggots as in the case

[13] A green violetear (*Colibri thalassinus*) feeding at the flowers of an *Elleanthus* species in the Monteverde Cloud Forest of Costa Rica.

of *Bulbophyllum phalaenopsis* and *Stelis villosa* or the buzzing activity of other flies around host material. Orchids pollinated by carrion flies have odors that mimic rotten flesh and often are dark red, dark brown or red-purple. A great many species of *Bulbophyllum* and *Masdevallia* appear to be pollinated by carrion flies.

Even termites and crickets may get into the act. The majority of *Angraecum* species endemic to the Mauritius and Reunion islands are clearly pollinated by something other than long-tongued Hawk moths as evidenced by their development of short-spurred, mostly green flowers. We now know that at least *Angraecum cadetii* is pollinated by a species of raspy cricket (Micheneau et al. 2010). The cricket, also new to science, represents the first clearly supported evidence of pollination by herbivorous orthopterans (grasshoppers, crickets and katydids) in the orchid family and in flowering plants in general. *Rhizanthella gardneri*, one



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[14–15] Bird-pollinated orchids often share similar urn- or tubular-shaped flowers. *Dendrobium secundum* [14] is known to be pollinated by birds. Although the pollinator of *Cryptochilus sanguineus* [15] is unknown, the urn-shape, bright red flowers and arrangement on the inflorescence all strongly suggest the pollinator to be a bird species.

Growers: [14] Smithsonian Institution, [15] Marni Turkel.

[16] Not all bird-pollinated orchids are tubular or urn-shaped. This *Cattleya*<sup>2</sup> *coccinea* is dramatically reduced in size from its larger, bee-pollinated relatives. The bright red color and narrow constricted lip are also both characteristic of the changes that result from adaptation to bird pollination. Grower: Anna S. Chai.

of Australia's curious underground orchids, appears to be regularly pollinated by termites, the only known example of termite pollination in the Orchidaceae (van der Cingel 2001). This rare and unusual orchid spends its entire life underground in association with the roots of a member of the genus *Melaleuca*. At flowering time, a head of small, spirally arranged flowers emerges from the ground but remains concealed under the leaf-litter. While pollination by a fungus gnat has been demonstrated, termites have also been observed to regularly and systematically visit newly opened flowers and to transport pollen masses making them likely pollinators.

While birds may not seem like likely orchid pollinators they are however, fairly regularly encountered. The syndrome for bird pollination is similar to that of butterfly pollination, with tubular, vividly colored red, yellow, violet or white keyhole-flowers except that the flowers are typically much stiffer and fragrance is usually absent. Bird pollination becomes more and more important with increasing altitude and may represent a natural progression as insects become less and less active at colder, higher elevations. In the Old World tropics, Sunbirds (Nectariniidae) are efficient pollinators and many species of *Dendrobium* are probably pollinated by these birds. In the New World tropics the role is filled by hummingbirds (Trochilidae). Examples of hummingbird-pollinated orchids include species of *Comparettia*, *Cochlioda*, and *Elleanthus* and *Epidendrum pseudepidendrum* (van der Cingel 2001). Lastly, not all bird-pollinated orchids are vividly colored. *Angraecum bracteosum* and *Angraecum striatum*, both endemic to the Island of Reunion off the coast of Madagascar, are pollinated by birds (Micheneau et al. 2008). The latter species is pollinated by

a variety of *Zosterops borbonicus* also endemic to Reunion Island and represents a great example of the evolutionary interdependence of orchid and pollinator. In bird pollination, the pollinia are usually attached to the beak and, at least in hummingbird pollinated orchids, a significant percentage of species have dark pollinia suggesting that natural selection has favored those with more difficult to see dark pollinia over those with typically more visible yellow pollinia.

Structural changes brought on by adaptation to pollinators can have such dramatic effect on flower form that closely related species may appear to belong to different genera and conversely, orchids not really closely related may produce very similar flowers — the result of convergent evolution. Such seems to be the case in the *Oncidium* alliance where a wide range of pollinators is operative. Historically, the generic limitations in this group of orchids have often been dominated by floral structural differences and we are now finding, based on DNA sequences, that this may not necessarily be correct. One interpretation of the data places a large number of closely related species from multiple genera into the genus *Oncidium* and conversely moves a group of species with otherwise *Oncidium*-like flowers into *Gomesa* (Chase et al. 2009). Basically flat, bright yellow-and-brown *oncidiums* appear to mimic the flowers of a group of plants in the Malpighiaceae. The flowers of these flowering trees and shrubs are bright yellow and one petal is modified into a structure called the banner petal. On the banner petal are specialized glands that produce thick brown oil. Pollination in this group of flowering plants is effected by oil-collecting bees of the genus *Centris*. These bees land on the banner petal and, while grasping this petal tightly, scrape the oil-producing glands. *Oncidiums* pollinated by *Centris* bees are bright yellow and often have brown markings that mimic oil-producing glands (in some *oncidiums*, actual oil glands are present on the side lobes or crest of the lip). When the pollinating bee lands to harvest the oil deposit, it firmly grasps the *oncidium's* lip with its mandibles while attempting to harvest oil from the flower. Such a pollination strategy requires a solid, strong connection between the orchid lip and the column or oil-harvesting runs the risk of destroying the flower. As such, the lip of these *Oncidium* species is fused to the column across the entire lip base. In contrast, bees of the genus *Bombus* (bumblebees), like honey bees, feed on nectar and collect

<sup>2</sup>Formerly *Sophranitis*.



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pollen to feed their larvae. These bees are attracted to floral structures that resemble or suggest the presence of nectar and pollen and in orchids this can take the form of yellow crests and yellow dusting of color against light flower color resembling spilt pollen and shallow cavities formed by the narrow attachment of the lip to column in some species. Nectar-feeding bees do not grasp the flower in the same way as oil-collecting bees while harvesting and in these cases the orchid lip may be attached to the column by just a narrow claw. Finally, adaptation to bird pollination results in the most dramatic changes. The current DNA data suggests that *Cochlioda* and *Symphoglossum*, whose bright red, pink and orange flowers look nothing like those of an *Oncidium*, are in fact just that — orchids pollinated by hummingbirds and even *Sigmatostalix*, a genus that at first glance seems distinctive, is nothing more than a scaled-down version that has specialized in the small end of the oil-collecting bee spectrum.

**FLORAL ATTRACTIONS** Any discussion of orchid pollination wouldn't be complete without a discussion of the mechanisms by which the pollinators are attracted to the flower. We've briefly touched on orchids that use fragrance to mimic rotting flesh but that's just the tip of the iceberg. No other plant family exhibits the range found in orchids: from real or perceived rewards (food or sex) to those with moveable parts or floral traps to those that attract pollinators based on mimicry of other flowers or insects. Food rewards, real or perceived, may represent the simplest of these attraction mechanisms. While orchid pollen isn't consumed by the insects that pollinate orchids, most *Polystachya* and some *Maxillaria* and *Eria* species have evolved mealy, pollenlike substitute that

forms on their lips. The pollinating insects, usually bees, eat this pseudopollen, thereby assuring that the bees will return to additional flowers (Dressler 1981). Alternatively, some *Maxillaria* species form waxes on their lip calluses that are collected by the pollinators for some purposes not clearly understood. The labellum of freshly opened *Dendrobium unicum* flowers is covered with fine trichome hairs that produce starch or sugar. These hairs are connected to the lip surface by a section of specialized cells that decompose as the flower ages. When the flowers are too old to be good candidates for pollination or are actually pollinated, these cells die and are sloughed off leaving a lip surface devoid of reward (Kjellson and Rasmussen 1987, Davies and Turner 2004). In some species, the promise of reward is hollow. The yellow crest of hairs in *Calypso*, *Arethusa* and *Calopogon* evidently resemble a cluster of pollen-bearing anthers and pollination depends on deceiving inexperienced bees.

Often the promise of rewards is also coupled with the presence of moveable parts. Such moving parts can be passive as in the fringes present on many *Bulbophyllum* flowers to those that spring shut (with or without the creation of a trap) when triggered by a pollinating insect. Fringes, hairs, tassels and other appendages may do nothing more than give the appearance of constant motion around the flower or they may provide more interest. In the case of *Bulbophyllum phalaenopsis*, the white structures on the flower resemble maggots and help to strengthen the impression of something dead. It has been suggested that the tassels present on the flowers of *Stelis villosa* are actually perceived by the pollinating insect as larval maggots on which their own larvae feed. Fringes and appendages may be coupled with moveable



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[17–19] Nowhere are the changes induced by pollinator more dramatic than those in the genus *Oncidium* sensu lato. Historically the taxonomy of this group of orchids has largely been based on floral morphology and modern DNA sequencing suggests that a number of genera, including *Oncidium*, *Odontoglossum* and *Cochlioda*, may indeed all be orchids. The yellow-and-brown *Trichocentrum stipitatum* [17] represents the group of Malpighiaceae-mimics pollinated by *Centris* bees that collect oil. *Odontoglossum crispum* [18] represents the changes that occur when the pollinators are pollen and nectar-feeding *Bombus* species and *Odontoglossum sanguineum* [19] is hummingbird pollinated. As in many epidendrums, the nectary in *Odm. sanguineum* is formed by fusion of the lip to the underside of the column. The entrance to this short chamber is visible in the face-on view [19A]. The up-turned aspect of the flower, common in bird-pollinated orchids, is seen in the side-on view [19B]. Grower [17]: Hawk Hill Nursery.





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pollinators to territorial insect species to sexual mimicry involving flowers that resemble females of the pollinating species. Some species of *Tolumnia* are believed to be mimics of Malpighiaceae. Female oil-gathering bees collect oil from the glands of the flowers of these vines and the same bees have been seen to seize *Tolumnia* species and then attempt to fly away (Nierenberg 1972). Such mimicry may be a fairly common occurrence. *Phragmipedium kovachii* is believed to mimic a species of *Tibochina*, *Phrag. besseae* appears to mimic a similarly-colored gesneriad and *Epidendrum ibaguense* appears to mimic both lantana and a milkweed species with orange-and-yellow flowers (Dressler 1981). In the last case, the mimicry may actually accomplish two things. Inexperienced insects may be fooled into visiting the *Epidendrum* flowers at a frequency sufficient to ensure reproductive success and herbivores may mistake them for the unpalatable species they resemble. In fact, there is an entire group of *Epidendrum* species that superficially resemble *Epi. ibaguense*, varying in color and details of the lip. Each of these species appears to mimic a different related shrub based on flower color. Recently, Du Puy and Cribb (2007) have suggested that *Cymbidium insigne* subsp. *seidenfadenii* is a floral mimic of *Rhododendron lyi*, a species with which it grows and flowers sympatrically. This subspecies is found in two forms, one with the characteristic red-marked white lip and a form devoid of red markings in the lip. The *Rhododendron* bears a white flower with a touch of yellow in the throat and freshly opening flowers of the three species appear remarkably similar. This *Cymbidium*, *Rhododendron* and *Dendrobium infundibulum* (a species which is also common in the same habitat) were observed to be visited by the same species of bumblebee, *Bombus eximius*, and pollinia from both orchid species was observed on the visiting bees. They suggest that the presence of the red-free color form in large numbers might be an excellent example of natural selection in process. This color form more closely resembles the *Rhododendron* flower when freshly opening and may be being selected for in the competition for pollinating bees.

Floral mimicry that depends on resemblance of an orchid's flowers to invading insects has been characterized by van der Pijl and Dodson as pseudoantagonism but it might be better called pseudotrespassing. This mimicry is observed in several species of *Oncidium* as well as possibly *Tolumnia henekenii*. The pollinator of

parts. A good example of this combination is the yellow fringe on the hinged labelum of *Calopogon* species that appears to the pollinating insect as edible pollen on a non-orchid flower. When the pollinating bee lands on the lip, the weight of the bee causes the lip to fall forward onto the column, transferring pollen.

Trap flowers run the gamut from passive traps such as *Cypripedium acaule* and *Phragmipedium besseae* to those with active traps such as *Pterostylis* and *Porroglossum*. Passive traps function by creating a single point of entry and a single escape route that brings the pollinating insect out past the flower's anther. The escape route can be created by a lining of aligned hairs that allow only one way out, surface texture that allows the pollinating insect to establish footing only along the appropriate route or stair like structures that force the insect past the anther. The elliptical "windows" around the rim of the pouch of *Phrag. besseae* are actually windows composed of colorless, transparent cells that are designed to allow sufficient light to enter the pouch to keep the trapped, diurnal insect active long enough to emerge from the pouch. Without them, the trapped insect would simply go to sleep and perhaps even die in the pouch. The most incredible example of passive traps in orchids is *Coryanthes* where the visiting euglossine bee, attracted by the powerful resinous fragrance, is maneuvered into a liquid-filled bucket from which the only escape for the now wet bee is out through a narrow channel at the back of the bucket. Bees too small simply leave the bucket without contacting the anther and bees too large cannot get out. When the bee exits the passageway, the pollinia attach pointed toward the back of the bee. Contact with the stigmatic cavity requires

[20] Sebastián Vieira observed this wasp inspecting every flower on the inflorescence of this *Pleurothallis* species in a forest in the mountains of Colombia. Evidently one of the "honest" species in this genus, the wasp was observed to lick the nectar from each flower for some seconds before proceeding to the next flower. In the process, the orchid's pollinaria were attached to the wasp's head.

that the pollinia be upright or pointed forward toward the bee's head. The orchid avoids this complication by the fact that the bee is wet when it leaves the escape route and cannot fly. As the bee dries, the pollinarium stipe dries as well and curls forward aligning the pollinia.

In several orchid species, the hinged lip movement is not passive in nature. The genus *Porroglossum* is a good example. In these orchids, the hinged lip is connected to the column by a long column foot and the lip is sensitive to touch at the callus near the base of the lip. When touched, the sensitive lip quickly snaps shut, creating a cavity between the lip and the ventral surface of the column trapping the visiting insect. The only exit is up along the lip surface past the stigma and rostellum. Insects too small to effect pollination either do not trigger the lip or simply leave through what for them is a wide open pathway. Insects that are too large may force their way out the side of the trap. A similar mechanism occurs in *Acostaea*, *Pterostylis* and some species of *Drakaea*.

**FLORAL MIMICRY** Orchids are masters of mimicry in the plant world. Floral mimicry in orchids ranges from mimicking other flowers to compete for

*Oncidium* species, such as *Oncidium sphacelatum* and *Oncidium ensatum*, appears to be the male of a species of oil-collecting bee. The females collect oil from clusters of plants and the males tend to pick these clusters as bases to defend their territories against any flying insects that are not females of their species. The inflorescences of these orchid species wafting in the breeze appear sufficiently like invading swarms of insects that the male bees attack the flowers and carry pollen away on their faces with the “border skirmish” to be repeated on other inflorescences within the territory. *Tolumnia henekenii*, endemic to the island of Hispaniola, was long thought to be pollinated by pseudocopulation because the flowers are visited by male bumblebees (Dod 1976). However, it now appears that the mechanism may be more likely pseudoantagonism. Bumblebees are terrestrial, territorial bees and typically occupy fiercely defended territories. The bumblebeelike flowers of this orchid are thought to resemble male bumblebees and pollination may result from attack on the flowers by the defending male bee.

The epitome of floral mimicry involves those cases where orchid flowers resemble females of the pollinating insect and pollination occurs as the result of pseudocopulation. Pseudocopulation in orchids has evolved multiple times in different parts of the world and with different groups of orchids and insects, and it’s remarkable that it appears to be found only in orchids. In some cases, the specificity is so well developed that natural hybrids are prevented while in other cases natural hybridization is relatively common. For instance, in European *Ophrys*, the resemblance is essentially visual and fairly unspecific. Recent genetic analyses suggest that of the 216 distinctly different taxa in this genus, 118 of them are of hybrid origin (World Checklist of Selected Plant Families 2011). This is in stark contrast to the situation observed for Australian terrestrial orchids, such as *Chiloglottis* and *Drakeae*. In these cases, the attraction of the male insect is pheromonal and reinforced visually. Natural hybrids in these genera are essentially nonexistent. In the Western Hemisphere, pseudocopulation has evolved in at least two orchid tribes, the Maxillarieae and the Epidendroideae. It is the main pollination syndrome in *Trichoceros* and *Telipogon* (both in the Maxillarieae tribe). Both are apparently pollinated by flies, the former by males of the genus *Paragymnomma* (van der Cingel 2001). It has recently been observed in *Lepanthes* (Blanco and Barboza 2005). In *Lepanthes*, the pollinator is a male fungus gnat



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[21] *Prasophyllum* is one of the few genera in the Diurideae known to attract its pollinators with the reward of nectar, the other genera invoking deceit or sexual mimicry. Pollinators, depending on species, are all manner of nectar-

seeking insects from bees and wasps to beetles and flies. Here *Lissopimpla excelsa*, known in Australia by the common name orchid dupe wasp, pollinates *Prasophyllum vitetrum*. The wasp is known as the orchid dupe because this species is duped into pollinating a *Cryptostylis* species by sexual mimicry. Like all members of its genus, *Lissopimpla excelsa* is parasitic.

[22] Some orchids combine pollinator syndromes. The pronounced crest on the lip of this *Calopogon* flower looks strikingly like a cluster of pollen-bearing anthers. In addition, the lip is hinged near its base so that when a feeding bee lands on the crest, the weight of the bee will cause the lip to collapse forward dropping the bee onto the column in the flower’s center.



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and we now know that at least in one group of Australian terrestrials, *Cryptostylis*, the encounters lead to ejaculation by the male insect (Gaskett et al. 2008). The cost of sperm wastage is fascinating and begs the question as to why these insects continue to visit these flowers. The pollinators of these Australian sexually-deceptive orchids are almost always solitary and haplodiploid species. Therefore, female insects deprived of matings by orchid deception can still produce male offspring, and as a result increase the percentage of males in the population and concurrently enhance orchid pollination.

In addition to these simple examples of mimicry in which an orchid species produces a fragrance suggestive of the female of the pollinating species or evolves a flower that looks like another species in order to compete for pollinators, some orchids express what might be called second-order mimicry. Mimicry of the second order is especially intriguing. In these second-order situations, the flower produces chemical or visual signals that suggest another insect, the presence of which attracts the pollinator to the flowers. As an example, *Epipactis veratrifolia* has dark structures on the labellum that superficially resemble a colony of black aphids. When aphid colonies are under attack by predatory insects, the aphids emit a chemical pheromone that alerts the remainder of the colony to the attack. This pheromone however, also attracts other predatory insects to the fray. In the case of this *Epipactis* species, the flower's fragrance is a chemical copy of the aphid-under-attack pheromone. The pollinating wasp sees the dark lumps on the labellum and smells aphid colony in distress and lands on the flower to feed on the aphid colony. As a result, orchid pollinia are transferred from flower to flower (Stöckl et al. 2010).

The more we study the world of orchid pollination, the more intricate and convoluted it becomes. Eventually, we may figure out the answer to that age old question, "Which came first, the chicken or the egg?" but in the meantime one thing is clear: form and function are intimately linked when it comes to orchid pollination. If you can imagine a pollination mechanism we will probably someday find an orchid that utilizes it.

#### References

- Adams, R.M. and G.J. Goss. 1976. The Reproductive Biology of the Epiphytic Orchids of Florida III. — *Epidendrum anceps* Jacquin. *Amer. Orchid Soc. Bull.* 45(6):488–492.
- Blanco, M. and G. Barboza. 2005. Pseudocopulatory Pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by Fungus Gnats. *Ann. Bot.* 95(5):763–772.
- Buchmann, S.L. 1987. The Ecology of Oil Flowers and

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[23–24] Sexual mimicry may take more than one route. Australian terrestrials such as this *Chiloglottis* species [23] mimic both sight and smell, producing fragrance compounds that mimic the sexual pheromones of the pollinating insect species. In these cases the combination of sight and smell make attraction exceptionally specific and natural hybrids in these systems are effectively unknown. On the other hand, in European terrestrials such as this *Ophrys* species [24] the mimicry appears to be strictly visual, the orchid appearing to the insect to be a female of its species. The deceit is not nearly perfect and as a result natural hybrids abound in European terrestrials.





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- Their Bees? *Annual Review of Ecology and Systematics*. Annual Reviews, Palo Alto. 18:343–96.
- Chase, M. and A. Pridgeon. 2009. Subtribe Oncidiinae, pp. 211–394. In *Genera Orchidacearum Vol. 5 Epidendroideae (Part Two)*, A.M. Pridgeon, P.J. Cribb, M.W. Chase and F.N. Rasmussen (eds.). Oxford University Press, Oxford.
- Coleman, E. 1928. Pollination of an Australian Orchid by the Male *Ichneumonid* *Lissopimpla semipunctata* Kirby. *Transactions of the Entomological Society of London* 76:533–539.
- . 1932. Pollination of *Diuris pedunculata* R.Br.? *Victorian Naturalist* 49:179–186.
- Davies, K.L. and M.P. Turner. 2004. Pseudopollen in *Dendrobium unicum* Seidenf. (Orchidaceae): Reward or Deception? *Ann. Bot.* 94:129–132.
- Dod, D.D. 1976. *Oncidium henekenii* — Bee Orchid Pollinated by Bee. *Amer. Orchid Soc. Bull.* 45(9):792–794.
- Dressler, R.L. 1981. *The Orchids, Natural History and Classification*. Harvard University Press, Cambridge and London.
- Du Puy, D. and P. Cribb. 2007. *The Genus Cymbidium, 2nd Edition*. Kew Publishing, Royal Botanic Gardens, Kew.
- Gaskett, A.C., C.G. Winnick and M.E. Herberstein. 2008. Orchid Sexual Deceit Provokes Ejaculation. *The American Naturalist* 171:E206–E212.
- Kjellson, G. and F.N. Rasmussen. 1987. Does the Pollination of *Dendrobium unicum* Seidenf. Involve Pseudopollen? *Die Orchidee* 38:183–187.
- Micheneau, C., J. Fournel, L. Humeau and T. Pailler. 2008. Orchid–Bird Interactions: A Case Study from *Angraecum* (Vandaeae, Angraecinae) and *Zosterops* (White-Eyes, Zosteropidae) on Reunion Island. *Botany* 86:1143–1151.
- Micheneau, C., J. Fournel, B.H. Warren, S. Hugel, A. Gauvin-Bialecki, T. Pailler, D. Strasberg and M.W. Chase. 2010. Orthoptera, A New Order of Pollinator. *Ann. Bot.* 105(3):355–364 doi: 10.1093/aob/mcp299.
- Mota Maues, M. 1998. Reproductive Phenology and Pollination of the Brazil Nut Tree (*Bertholettia excelsa* Humb. & Bompl. Lecythidaceae) in Eastern Amazonia, p. 208. In *Pollinating Bees — The Conservation Link Between Agriculture and Nature*, eds. P.G. Kevan and V.L. Imperatriz-Fonseca. Ministério do Meio Ambiente, Brasília.
- Nash, R.C. 1979. Observation of Native Bees on *Diuris pedunculata*. *Journal of the Native Orchid Society of South Australia* 3:7–9.
- Nierenberg, L. 1972. The Mechanism for the Maintenance of Species Integrity in Sympatrically Occurring Equitant Oncidiids in the Caribbean. *Amer. Orchid Soc. Bull.* 41(10):873–881.
- Stökl, J., J. Brodmann, A. Dafni, M. Ayasse and B. Hansson. 2010. Smells Like Aphids: Orchid Flowers Mimic



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- Aphid Alarm Pheromones to Attract Hoverflies for Pollination. *Proceedings of the Royal Society B*, Online, DOI: 10.1098/rspb.2010.1770.
- Thien, L.B. and F. Utech. 1970. Thien, L.B., and F. Utech. The Mode of Pollination in *Habenaria obtusata* (Orchidaceae). *Amer. J. Bot.* 57:1031–1035.
- van der Cingel, N.A. 2001. *An Atlas of Orchid Pollination, America Africa Asia and Australia*. A.A. Balkema, Rotterdam.
- van der Pijl, L. and Dodson, C.H. 1966. *Orchid Flowers: Their Pollination and Evolution*. University of Miami Press, Coral Gables.
- Whigham, D.F. and McWhety, M. 1980. Studies on the Pollination Ecology of *Tipularia discolor* (Orchidaceae). *Amer. J. Bot.* 67(4):550–555.
- World Checklist of Selected Plant Families. 2011. The Board of Trustees of the Royal Botanic Gardens, Kew. Published on the Internet; <http://apps.kew.org/wcsp/> accessed 2011.
- Ron McHatton, PhD, has been growing orchids for more than 47 years. A chemist by training, he is the Society's chief operating officer, director of education and editor of its monthly e-newsletter. (e-mail [rmchatton@aos.org](mailto:rmchatton@aos.org)).

- [25] Pollination of *Diuris behrii* is not well understood. Visitation by only males of one bee species while other similarly colored species are ignored are aspects of sexual mimicry while the flower's bright yellow color and floral structures are indicative of nectar mimicry (Coleman 1932, Nash 1979).
- [26] *Cryptostylis leptochila*, the small-tongued orchid, is pollinated by male *Lissopimpla semipunctata* wasps. The wasps are common throughout Australia but the orchid is endemic to New South Wales and Victoria States. If the orchid is introduced to an area where it is new the male wasps detect the flowers almost immediately and are drawn to them (Coleman 1928).