

POLLINATION OF SLIPPER ORCHIDS (CYPRIPEDIOIDEAE): A REVIEW

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ABSTRACT. Cyripedioideae (five genera; ca. 176 species) are widespread in temperate and tropical Asia and America. About a quarter (42) of the species have been studied to determine their pollinators and/or breeding systems. All flowers are one-way traps pollinated by insects of particular types and size. Slipper orchids are self-compatible and pollinated by deceit. Most *Cypripedium* species are pollinated by bees, whereas some smaller-flowered species are pollinated by flies, and a few are pollinated by both. Most bee-pollinated *Cypripedium* species appear to be generalized food mimics. The fly-pollinated species have evolved diverse pollination systems that utilize a variety of flies as pollen vectors, including fruit flies, dung flies, and a fungal spore-eating hoverfly (Syrphidae). Most species of the tropical Asian *Paphiopedilum* and tropical American *Phragmipedium* are pollinated by hoverflies; flowers of many species in both genera have aphid-like spots that attract gravid female hoverflies that normally lay their eggs in aphid colonies. The more brightly colored *Paphiopedilum micranthum* and *Phragmipedium besseae* are pollinated by Hymenoptera. Autogamy is limited but occurs most frequently in *Phragmipedium* species. About two-thirds of the insect-pollinated slipper orchids (25/37) have evolved highly specialized flowers that are pollinated by a single pollinator or several pollinator species in the same genus. Species belonging to the same taxonomic section usually have the same pollination system. The deceit-pollination system of Cyripedioideae appears to have evolved early in diversification of Orchidaceae..

KEY WORDS: *Cypripedium*, *Mexipedium*, *Phragmipedium*, *Paphiopedilum*, *Selenipedium*

Introduction

Slipper orchids (Orchidaceae: Cyripedioideae) include five genera. Most *Cypripedium* species (52 spp.) are distributed in temperate areas of northeast Asia, North America including Mexico, and Europe (Cribb 1997a; World Checklist of Selected Plant Families 2013). *Paphiopedilum* (92 spp.) occurs primarily in tropical and subtropical southeast Asia (Cribb 1987, 1997a; World Checklist of Selected Plant Families 2013). *Phragmipedium* (26 spp.) species are restricted to tropical/subtropical central and South America (Pridgeon *et al.* 1999, World Checklist of Selected Plant Families 2013); *Selenipedium* (5 spp.) occurs in Panama and northern South America (Pridgeon *et al.* 1999; World Checklist of Selected Plant Families 2013), and the monospecific *Mexipedium xerophyticum* (Soto Arenas, Salazar & Hågsater) V.A. Albert & M.W. Chase is endemic to Mexico (Albert and Chase 1992). Cyripedioideae and Apostasioideae are the oldest subfamilies of Orchidaceae (Dressler 1981; Pridgeon *et al.* 1999).

Slipper orchids live in diverse climatic zones and habitats including subalpine forests (*Cypripedium* in China), cloud forests (*Phragmipedium* in the Andes), temperate forests (*Cypripedium* in North America, northeast Asia, and Europe), tropical and subtropical forests (*Paphiopedilum* in Southeast Asia), bogs (*C. reginae* in North America), and even tundra (*C. passerinum* in North America). Flowers vary greatly in size from the Chinese *C. bardolphianum* with thumbnail-sized flowers to the 12-cm-wide flowers of Peru's *Phragmipedium kovachii* J.T. Atwood, Dalström & Ric.Fernández (Atwood *et al.* 2002).

Of the 176 recognized slipper-orchid species (World Checklist of Selected Plant Families 2013), 42 have been subjects of pollination studies (Table 1). The insect-pollinated species include 22 from *Cypripedium*, 12 from *Paphiopedilum*, and six from *Phragmipedium*. *Selenipedium* and *Mexipedium* are unstudied. Four are autogamous, including the subarctic *C. passerinum* (Catling 1990) and three from *Phragmipedium*: *P. reticulatum*, *P.*

lindenii (Pemberton 2011; Koopowitz 2008), and *P. boissertianum* (Pridgeon *et al.* 1999).

Pollination mechanism

Despite their wide geographical distribution, diverse habitats, and sizes, all species have the same basic floral morphology and pollination mechanism (Cribb 1987, 1997b; Bernhardt and Edens-Meier 2010; Edens-Meier *et al.*, in press). Species are self-compatible but require insects to transfer pollen from the anther to the stigma (Edens-Meier *et al.* 2011). None of their flowers is known to produce nectar or other rewards for pollinators and so are pollinated by deceit (Nilsson 1979; Edens-Meier *et al.*, in press). The lip is expanded into a pouch with a dorsal opening, a distinctive feature that is readily recognized. A small lateral opening on each side of the lip is created by the interlocking bases of the lip and column. The two anthers are positioned on either side of the column inside each lateral opening. Potential pollinators enter the lip's dorsal opening and become trapped inside. The only escape is through one of the lateral openings at the base of the lip. To reach either of these openings, the insect crawls on the interior of the pouch upward toward the stigma, which is positioned with its receptive surface facing the inner surface of the lip. The insect must then squeeze beneath the stigma's receptive surface. If the insect carries pollen, it would be on the dorsal surface of its thorax. Papilli on the stigma scrape the pollen from the insect as it moves beneath. After passing beneath the stigma, the insect reaches one of the anthers at a lateral opening. To escape, the insect must squeeze beneath the anther, receiving a pollen smear or mass applied to its thorax.

In order for a trapped insect to be a pollinator, it must be of a particular size that enables it to squeeze beneath the stigma and the floor of the lip and then beneath the anther and out of through a lateral opening (Bänziger 2005; Li *et al.* 2008a, b). This mechanism assures both pollen delivery and pollen removal. If the insect is too large, which usually means that its thorax is too thick, it cannot escape. Such an insect will usually die inside the lip or become stuck in a lateral opening (Pemberton 2011), but some bumblebees (*Bombus*) are able to escape

through the dorsal opening. If, on the other hand, the insect is too small, it easily passes beneath the stigma and an anther without contacting either, neither delivering nor removing pollen during its escape. Although species are self-compatible, the position of the stigma and anthers and the unidirectional movement of the pollinator beneath the stigma and anther prevent self-pollination. Self-pollination would be possible if the pollinator re-enters a flower previously visited or a different flower on the same plant, but after the pollinator's arduous escape, it usually flies quickly away from the flower and the area. However, individual *Lasioglossum* bees have been recorded re-entering previously visited flowers of *C. henryi* in China (Li *et al.* 2008b).

Cypripedium pollination

Cypripedium species diverged earlier than the other genera (Guo *et al.* 2012) and have the greatest diversity of pollination systems and pollinator types. Pollination by large bees, all *Bombus* spp., occurs in five large-flowered *Cypripedium* species (section *Cypripedium*). Four of these species are pollinated by *Bombus* queens (rather than workers). One of these, *C. tibeticum* (Fig. 1), lives at in the high-elevation boreal zone in mountains of southwestern China. Its large purple flowers have a lip with a dorsal opening that appears to be black, and the lip often touches or is close to the ground. Mated queen bumblebees emerge from winter hibernation and search for nest sites, which are usually mouse holes. It is thought that the black dorsal opening of the lip resembles a mouse hole. A queen looking for a nest site enters the lip of the flower, becomes trapped, and pollinates it as it escapes. This hypothesis of nest-hole deceit is supported by the fact that none of the queen pollinators carries any provision for its young (pollen or nectar), which means that it has not yet established a nest and so is still searching for a suitable nest site (Li *et al.* 2006). All but a few *Cypripedium* species pollinated by bees belong to section *Cypripedium*. These orchids are colorful and often have fragrance (Barkman *et al.* 1997), indicating that they are generalized mimics of food-reward flowers.

Bees pollinators of slipper orchids are polylectic, meaning that they seek and gather the pollen of flowers



FIGURE 1. *Cypripedium tibeticum* flowers in China's Sichuan Province in China are pollinated by queen bumblebees searching for nest sites (Li *et al.* 2006). The dark entrance of the lip and the position of the flower near the ground are thought to mimic a mouse hole, a common nest site. The queen enters the lip, becomes trapped, and escapes by squeezing beneath the stigma and then an anther at one the lateral openings at the junction of the bases of the lip and petals, delivering and removing pollen in the process. This trap-lip pollination mechanism occurs in all slipper orchids. Most *Cypripedium* species are pollinated by bees but diverse types of flies have recently been found to be the pollinators of small-flowered species.

belonging to diverse species (Edens-Meier *et al.*, in press), a characteristic that facilitates their attraction and entrapment. Eight *Cypripedium* species are pollinated by small bees belonging to different bee families. The most important bee family is Halictidae (sweat bees), followed by the Andrenidae (mining bees). A few bee species of minor importance belong to the Megachilidae (leaf-cutter bees), Colletidae (plaster bees), and Apidae (varied bees including bumblebees and honeybees). It is notable that honeybee pollination has been detected in only a single species of *Cypripedioideae*, the North American *C. reginae*, which has diverse pollinators; honeybees are not native to North America. Bees in Halictidae and Andrenidae are the sole pollinators of some *Cypripedium* orchids. The halictid pollinators belong to four genera with *Lasioglossum* species being

the most important. *Lasioglossum* bees are the sole pollinators of four *Cypripedium* species, as well as being part of the bee guild pollinators of an additional four *Cypripedium* species. The genus *Lasioglossum* is nearly pandemic (Michener 2000), and species in this genus pollinate *Cypripedium* in Asia, North America, and Europe. *Andrena* is a Holarctic genus with species that pollinate *Cypripedium* in Asia, North America, and Europe (Michener 2000). Sister *Cypripedium* species occurring in China and North America share pollination characteristics. Both *C. flavum* (China) and *C. reginae* (North America), both in section *Cypripedium*, are generalists employing bees and flies as pollinators. *Cypripedium plectrochilum* (China) and *C. arietinum* (North America), both in section *Arietinum*, have similar and unusual floral morphologies, and both are pollinated only by *Lasioglossum* bees.

Wasps are known to pollinate the strange flowers of *C. fasciculatum* (North America; section *Emantiopetalum*) in an odd case of brood-site deception. The small, brown flowers produce a mushroom-like odor that attracts several species of diapiiid wasp parasitoids in the genus *Cinetus* (Ferguson and Donham 1999). This wasp's developmental hosts are larvae of tiny fungus flies that breed in mushrooms. Female wasps apparently become trapped in the flowers while searching for fungus-fly larvae in which to oviposit.

All of the fly-pollinated *Cypripedium* species occur in China. Of these, *C. flavum* is unique in being pollinated by a mix of *Andrena* bee species, bumblebee workers, and blow flies that breed in carrion (Bänziger *et al.* 2005; Zheng *et al.* 2011). The other fly-pollinated *Cypripedium* species are narrow specialists, having highly evolved flowers that mimic the materials in which their pollinators breed. Molecular research indicates that these fly-pollinated, small-flowered orchids are in different sections of the genus (Li *et al.* 2011) and are not sister taxa. *Cypripedium bardolphianum* and *C. micranthum* (section *Sinopedilum*) are pollinated by fruit flies (*Drosophila* spp.) that breed in decaying fruit (Zheng *et al.* 2010). Their flowers are dark and smell of decaying fruit. True pollinaria (instead of soft pollen masses or sticky pollen smears as in most slipper orchids) occur in the flowers of both *C. bardolphianum* and *C. micranthum* (Perner 2009; Li *et al.* 2012).

This is astonishing given that pollinaria were thought to occur only in more advanced orchids (Dressler 1981). As the fruit fly moves beneath an anther, the pollinarium is attached to the dorsal area of its thorax. *Cypripedium sichuanense* (section *Trigonopedia*) is pollinated by a dung fly (Li *et al.* 2012), but why the fly is attracted to the purple, vividly marked flowers is not understood. *Cypripedium fargesii* (section *Trigonopedia*) is pollinated by a hoverfly (also called flowerflies, Syrphidae) in the genus *Cheilosia* that eats and disperses spores of fungi that infect leaves (Ren *et al.* 2011, 2012). The fly is attracted to the large hairy patches on the orchid's leaves that resemble fungal infections. Odor molecules associated with *Cladosporium* fungal cultures have been isolated from the orchid's fragrance. This mimicry of fungus-infected foliage to achieve pollination is one of the most bizarre cases in orchid pollination ecology. Fly pollination in most of these small-flowered *Cypripedium* species has been studied only recently, and such research has broadened our concept of pollination in temperate zone species.

***Paphiopedilum* pollination**

Paphiopedilum species that have been studied are mostly pollinated by hoverflies (Table 1). The flowers of these species are usually drably colored shades of green, brown, and maroon and are marked with spots, stripes, and hairs (Cribb 1987, 1997a), characteristics that are known to be attractive to flies (van der Cingel 2001). The staminodes of the flowers are often large and yellow, a color that contrasts to the other floral parts (Cribb 1987, 1997a). Furthermore, the staminodes usually have distinctive markings or bumps on their outer faces. The staminode of the Chinese *P. dianthum* bears small, light-colored spots, whereas the staminode in *P. villosum* from Thailand bears a raised wart or bump and a shiny surface (Bänziger 1996). The gravid female hoverfly pollinators appear to interpret these staminodes as aphid colonies, which are sought by these particular hoverfly females to lay eggs in for their aphid-eating larvae. Similarly, a wart might be interpreted by the fly as a single large, female aphid that is starting a new colony. Hoverflies are also attracted to honeydew (Henderson 1982), the sweet exudate produced by

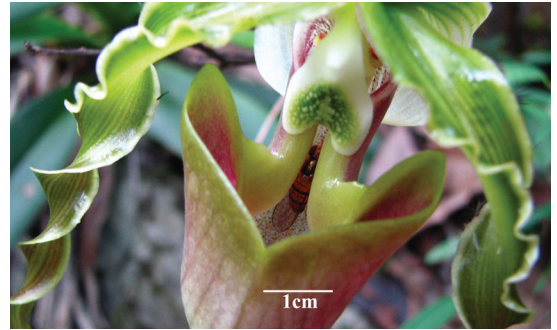


FIGURE 2. *Paphiopedilum dianthum* flower about to be pollinated by a female hoverfly in the genus *Episyrphus* in Guanxi Province in southwestern China (Shi *et al.* 2007). Eleven of the 13 studied *Paphiopedilum* species are pollinated by hoverflies, most of which are gravid females in brood-site pollination.

aphids, which shiny staminodes probably mimic. This mimicry of aphid colonies is so effective that hoverfly eggs have been found on and in the labellum, as seen in *P. rothschildianum* (Atwood 1994). The uniformly dull, light brown or white coloration of the flowers of *P. bellatulum* (section *Brachypetalum*) is different than other hoverfly-pollinated *Paphiopedilum* species, but the flower's dense, contrastingly-colored spotting probably attracts the flies. Some hoverfly-pollinated *Paphiopedilum* species such as *P. dianthum* (Fig. 2) are extreme specialists, being pollinated by a single hoverfly species (an *Episyrphus* species; Shi *et al.* 2007). Others such as *P. hirsutissimum* are specialists but are pollinated by several hoverfly species (Shi *et al.* 2009). Hoverfly-pollinated species belong to four subgenera (*Brachypetalum*, *Polyantha*, *Paphiopedilum*, *Sigmatopetalum*). The only studied *Paphiopedilum* species not exclusively pollinated by hoverflies are *P. micranthum*, which is pollinated by several bumblebees (Edens-Meier *et al.*, in press), and *P. armeniacum*, which is pollinated by several bees and a hoverfly (Liu *et al.* 2005). The colors of the flowers of these species in subgenus *Parvisepalum* are brighter than those of most hoverfly-pollinated *Paphiopedilum* species. *Paphiopedilum armeniacum* is bright yellow, whereas *P. micranthum* usually has a pink or white lip and a yellow staminode that contrasts with the colors of the petals and sepals. Yellow is attractive to bees, and most bee-pollinated flowers are yellow or blue (Paracer 2000). *Paphiopedilum armeniacum* is the

only studied *Paphiopedilum* having a generalized pollination system, with both bees and hoverflies as pollinators. Other brightly colored *Paphiopedilum* species are probably also pollinated by Hymenoptera.

Phragmipedium pollination

Little research has been done on the pollination of *Phragmipedium* species. Three of six examined species have flowers that are completely autogamous (Pridgeon *et al.* 1999; Pemberton 2011). *Phragmipedium lindenii*, the strange lipless species, has triandrous flowers with the extra anther appressed to the stigma. The stigma of *P. reticulatum* flowers is expanded laterally and backward so that it contacts the anthers. *Phragmipedium lindenii* and *P. reticulatum* plants have been observed to set fruit in 100% of their flowers (Pemberton 2011). *Phragmipedium boisserianum* is the third autogamous species, and some autogamy has also been observed in *P. schlimii* (Linden ex Rehb.f.) Rolfe (Pridgeon *et al.* 1999) and *P. longifolium* (Koopowitz 2008).

Three of the four insect-pollinated *Phragmipedium* species are narrow specialists, being pollinated by a single insect species. *Phragmipedium pearcei* and *P. caudatum* are each pollinated by female hoverflies of a single species (Pemberton 2011). *Phragmipedium longifolium* is pollinated by both a female hoverfly and a halictid bee (Dodson 1966; Pemberton 2011), although as previously mentioned some plants of this species are autogamous (Koopowitz 2008). The hoverfly-pollinated species (sections *Himantopetalum*, *Lorifolia*, and *Phragmipedium*) have dull-colored, green-and-brown flowers with aphid-like spots on the infolded surface of the lip above the dorsal opening or around the margin of the opening. I observed *Ocyptamus antiphales* (Walker), the female hoverfly pollinator of *P. pearcei* (Fig. 3), fly directly to these aphid-like spots then ricochet into the dorsal opening of the lip (Pemberton 2011). This brood-site pollination in *Phragmipedium* is remarkably similar to the hoverfly-pollinated *Paphiopedilum* species in Asia.

Flowers of *Phragmipedium besseae* are bright red/orange or scarlet and have a velvety surface. Ever since the sensational discovery of *P. besseae* in 1981 (Koopowitz 2008), there has been curiosity and speculation about what pollinates its red flowers, which

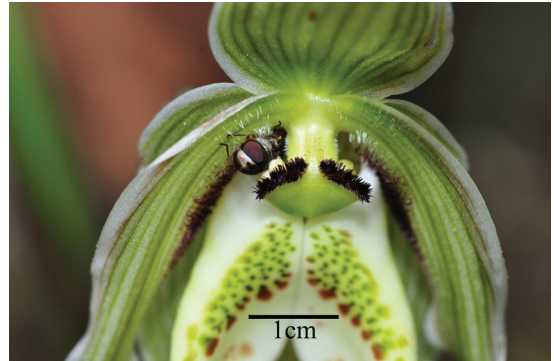


FIGURE 3. *Phragmipedium pearcei* flower being pollinated by a female hoverfly, *Ocyptanthes antiphales*, in Ecuador (Pemberton 2011). Hoverflies appear to be the pollinators of most drably colored *Phragmipedium* species in brood-site pollination. This hoverfly and other hoverfly pollinators of both *Phragmipedium* and *Paphiopedilum* species appear to be attracted to aphid-like spotting on the flowers. These hoverflies lay their eggs in aphid colonies for their aphid-eating larvae. females in brood-site pollination.

are unique in cyripediooid orchids. Hummingbirds have been hypothesized as the pollinators (Atwood *et al.* 2002; Fisher 2011) because they pollinate many red-colored flowers of diverse families in tropical America (Rodriguez-Girones & Santamaria 2004). However, the flowers of *P. besseae* are clearly traps for insect pollinator(s) as in all slipper orchids. In addition to the trap morphology, other features indicate insect pollination. The internal margin of the dorsal entrance to the lip is slippery, which facilitates insect capture. The internal surface of the pouch has a central row of hairs leading to the stigma, serving as a ‘stairway’ for insects. Windows in the upper portion of the lip appear to direct captured insects up and back towards the stigma (Fisher 2011). Hummingbirds are, of course, are too large to be trapped. If they probed the lateral openings, the beak could contact the anthers but would be unlikely to reach the receptive surface of the stigma. Flowers of *P. besseae* are pollinated by an undetermined species of tiphiid wasp (Pemberton, unpubl.). Tiphiid wasps are parasitoids of subterranean scarab larvae (O’Neill 2001).

Wasp pollination of the red-colored *Phragmipedium besseae* is a paradox because it appears that Hymenoptera as well as most insects (with the exception of butterflies) are visually

insensitive to red and have difficulty distinguishing red flowers from green leaves (Rodríguez-Girones & Santamaria 2004). Red is thought to have evolved in bird-pollinated flowers to make them unapparent to insects that could deplete their nectar (Rodríguez-Girones & Santamaria 2004). There is some yellow coloration on the rim of the dorsal entrance of the lip that might attract Hymenoptera to the trap entrance. *Phragmipedium besseae* belongs to section *Micropetalum* (Koopowitz 2008), which contains species with colorful flowers having velvety surfaces, unlike the green-brown *Phragmipedium* species pollinated by hoverflies. The appearance of these flowers indicates that they, like *P. besseae*, are pollinated by Hymenoptera. The magnificent flowers of the recently discovered *P. kovachii* are probably pollinated by large bees, given their large size, fuchsia-purple coloration, and contrasting white to yellow staminode.

There appears to be convergent evolution in *Phragmipedium* and *Paphiopedilum*. The majority of the species in both genera have evolved brood-site pollination by female hoverflies, with their dull-colored flowers and aphid-like spotting above the dorsal opening. The aphid-like spotting is on the staminode in *Paphiopedilum* species and the folded lip in *Phragmipedium*, but the function appears to be the same in both genera. Pollinators of brightly colored *Phragmipedium* and *Paphiopedilum* have been determined in only one species in each genus, and both are pollinated by Hymenoptera.

Selenipedium and *Mexipedium*

Pollination of *Selenipedium* species has not been studied in detail. I observed the flowers in a population of *S. aequinoctiale* Garay in Ecuador for three days in 2010. Although fruits were present on some plants, no insect visitors were seen. This was probably due to the variable weather with periods without sun and the presence of only a few short-lived flowers on scattered plants, which made observing more than one or two flowers at a time difficult. Dodson (2003) observed an *Anthophora* bee emerging from a flower of this species, but pollination was apparently not seen or documented (Edens-Meier *et al.*, in press).

Pollinators have also not been observed on flowers

of *Mexipedium*. Some fruits have been seen on plants (Soto *et al.* 1990), but because many flowers did not set fruit, the species is unlikely to be autogamous. The flowers are small, white, some with a pink flush, and velvety, as in those of section *Micropetalum* of *Phragmipedium*. Floral morphology is unlike that of fly-pollinated Cyripedioideae, and small bees are probably vectors.

Conclusions

Most cyripediooid orchids are specialists, having flowers that evolved to attract either bee or fly pollinators. Phylogenetic relationships are usually predictive of pollination systems; species belonging to the same taxonomic section usually have the same pollination system. Fifteen species are pollinated solely by bees and 16 species solely by flies. Fourteen *Cyripedium* species are bee-pollinated, compared to four pollinated by flies. In contrast, ten *Paphiopedilum* species are fly-pollinated, whereas only one is bee-pollinated (Table 1). *Phragmipedium* species appear to be mostly fly-pollinated, but few species have been studied. Five species have generalist pollination systems employing both bees and flies: *Cyripedium flavum*, *C. montanum*, *C. reginae*, *Paphiopedilum armeniacum*, and *Phragmipedium longifolium*. Two species, *C. fasciculatum* and *Phragmipedium besseae*, are pollinated by wasps.

Within the bee- or fly-pollinated species, degree of pollinator specialization varies considerably. Narrow specialization, defined here as genus-level specialization (multiple pollinator species in the same genus), occurs in eight species. Extreme specialization, in which a single insect pollinates a species, has evolved in 17 taxa. Most studied species (25 of 42) have highly evolved floral morphologies and attractants that allow a tiny proportion of the potential pollinators in their environments to be effective pollinators.

The success of the trap-lip pollination system in Cyripedioideae can be evaluated in terms of reproductive success. Fruit set in *Cyripedium* orchids is highly variable even within the same species and the same population during different years. For instance, fruit set in a population of *C. parviflorum* in Quebec, Canada, ranged from 22-75% during a four-year

TABLE 1. Pollinators of Cyripedioideae. Adopted and modified from Edens-Meier *et al.* (in press).

Species	Pollinator types and species	References
<i>Cyripedium acaule</i> Aiton	Bumblebees: <i>Bombus</i> spp. (queens)	Stoutamire 1967; Primack & Stacy 1998; Davis 1986
<i>C. arietinum</i> R.Br.	Bee: <i>Lasioglossum</i> sp.	Stoutamire 1967
<i>C. bardolphianum</i> W.W.Sm. & Farrer	Fruit flies: <i>Drosophila</i> spp.	Zheng <i>et al.</i> 2010
<i>C. calceolus</i> L.	Bees: <i>Andrena</i> spp.; <i>Lasioglossum</i> spp.; <i>Nomada</i> sp.; <i>Colletes</i> sp.	Nilsson 1979; Kull 2008; Antonelli <i>et al.</i> 2009
<i>C. candidum</i> Muhl. ex Willd.	Bees: <i>Andrena</i> sp.; <i>Halictus</i> spp.; <i>Lasioglossum</i> spp.; <i>Augochlorella</i> sp.	Catling & Knerer 1980
<i>C. fargesii</i> Franch.	Hoverfly: <i>Cheilosia</i> sp.	Ren <i>et al.</i> 2011; Ren <i>et al.</i> 2012
<i>C. fasciculatum</i> Kellogg	Wasp parasitoids: <i>Cinetus</i> spp. (females)	Ferguson & Donham 1999
<i>C. flavum</i> P.F.Hunt & Summerh.	Bees: <i>Andrena</i> spp. Bumblebees: <i>Bombus</i> spp. (workers); Blow fly: <i>Calliphora</i> sp.	Bänziger <i>et al.</i> 2008; Zheng <i>et al.</i> 2011
<i>C. guttatum</i> Sw.	Bees: <i>Lasioglossum</i> spp.	Bänziger <i>et al.</i> 2005
<i>C. henryi</i> Rolfe	Bees: <i>Lasioglossum</i> spp.	Li <i>et al.</i> 2008b
<i>C. japonicum</i> Thunb.	Bumblebees: <i>Bombus</i> spp. (queens)	Sun <i>et al.</i> 2009
<i>C. macranthos</i> Sw.	Bumblebees: <i>Bombus</i> spp. (queens)	Sugiura <i>et al.</i> 2002
<i>C. micranthum</i> Franch.	Fruit flies: <i>Drosophila</i> spp. (1?)	Li <i>et al.</i> 2012
<i>C. montanum</i> Thunb.	Bees: <i>Andrena</i> spp.; <i>Ceratina</i> sp.; <i>Halictus</i> sp.; <i>Lasioglossum</i> spp.	Vance, unpubl.
<i>C. parviflorum</i> Salisb.	Bees: miscellaneous, small; <i>Osmia</i> , <i>Andrena</i>	Curtis 1954; Light & MacConaill 2006
<i>C. passerinum</i> Richardson	Autogamous	Catling 1990
<i>C. plectrochilum</i> Franch.	Bees: <i>Lasioglossum</i> spp.; <i>Ceratina</i> sp.	Li <i>et al.</i> 2008a
<i>C. reginae</i> Walter	Bees: <i>Apis</i> sp.; <i>Hoplitis</i> sp.; <i>Megachile</i> sp.; <i>Anthophora</i> ; hoverflies: <i>Syrphus</i> spp.? scarab beetle: <i>Trichiotinus</i> spp.?	Edens-Meier <i>et al.</i> 2011; Vogt 1990
<i>C. sichuanense</i> Perner	Dung fly: <i>Scathophaga</i> spp.	Li <i>et al.</i> 2012
<i>C. smithii</i> Schltr. (= <i>C. calicicola</i> Schltr.)	Bumblebees: <i>Bombus</i> spp.	Li & Luo 2009
<i>C. tibeticum</i> King ex Rolfe	Bumblebees: <i>Bombus</i> spp. (queens)	Li <i>et al.</i> 2006
<i>C. yunnanense</i> Franch.	Bee: <i>Lasioglossum</i> sp.	Bänziger <i>et al.</i> 2008
<i>Paphiopedilum armeniacum</i> S.C.Chen & F.Y.Liu	Bees: <i>Lasioglossum</i> sp.; <i>Ceratina</i> sp.; hoverfly: <i>Eristalis</i> sp.	Liu <i>et al.</i> 2005
<i>P. barbigerum</i> Tang & F.T.Wang	Hoverflies: <i>Allograpta</i> sp.; <i>Erisyrphus</i> sp.	Shi <i>et al.</i> 2008
<i>P. bellatulum</i> (Rchb.f.) Stein	Hoverflies: Syrphidae	Bänziger 2002
<i>P. callosum</i> (Rchb.f.) Stein	Hoverflies: Syrphidae	Bänziger 2002
<i>P. charlesworthii</i> (Rolfe) Pfitzer	Hoverflies: Syrphidae	Bänziger 2002
<i>P. dianthum</i> Tang & F.T.Wang	Hoverfly: <i>Episyrphus</i> sp.	Shi <i>et al.</i> 2007
<i>P. hirsutissimum</i> (Lindl. ex Hook.) Stein	Hoverflies: <i>Allobaccha</i> sp.; <i>Episyrphus</i> sp.	Shi <i>et al.</i> 2009
<i>P. parishii</i> (Rchb.f.) Stein	Hoverfly: <i>Allograpta</i> sp.	Bänziger 2002
<i>P. micranthum</i> Tang & F.T.Wang	Bumblebees	Edens-Meier <i>et al.</i> (in press)
<i>P. purpuratum</i> (Lindl.) Stein	Hoverfly: <i>Ischiodon</i> sp.	Liu <i>et al.</i> 2004
<i>P. rothschildianum</i> (Rchb.f.) Stein	Hoverfly: <i>Dideopsis</i> sp.	Atwood 1994
<i>P. villosum</i> (Lindl.) Stein	Hoverflies: <i>Betasyrphus</i> sp.; <i>Episyrphus</i> sp.; <i>Syrphus</i> sp.	Bänziger 1996
<i>Phragmipedium besseae</i> Dodson & J.Kuhn	Wasp parasitoid: Tiphidae sp.	Pemberton, unpubl.
<i>P. boisserianum</i> (Rchb.f. & Warsz.) Rolfe	Autogamous	Pridgeon <i>et al.</i> 1999
<i>P. caudatum</i> (Lindl.) Rolfe	Hoverfly: <i>Syrphus</i> sp.	McCook 1989; Pemberton 2011
<i>P. lindenii</i> (Lindl.) Dressler & N.H.Williams	Autogamous	Pemberton 2011
<i>P. longifolium</i> (Warsz. & Rchb.f.) Rolfe	Bee: <i>Chlerogella</i> sp.; Hoverfly: <i>Syrphus</i> sp.	Dodson 1966 Pemberton 2011
<i>P. pearcei</i> (Veitch ex J.Dix) Rauh & Senghas	Hoverfly: <i>Ocyrtamus</i> sp.	Pemberton 2011
<i>P. reticulatum</i> (Rchb.f.) Schltr.	Autogamous	Pemberton 2011

rarely set fruit (Primack & Stacy 1998). Rewardless orchids usually have lower levels of fruit set than do orchids with rewards (Tremblay *et al.* 2005). Fruit set in Cyripedioideae, as in many other long-lived orchids, is often low, but the large numbers of seed per capsule and the longevity of the plants probably compensates. The trap-lip pollination system that efficiently removes and places pollen on captured and escaping insects appears to be successful given the persistence of Cyripedioideae through time and their wide radiation. Much of this success is probably due to the evolution of specific flower forms, coloration, and odors that enable them to attract and use specific insect species or types as pollinators in diverse habitats and climatic zones.

The pollination ecology of the majority of this subfamily (ca. 120 species) is unknown. Recent studies of small-flowered Chinese *Cypripedium* species and Ecuadorian *Phragmipedium* species have led to the discovery of unique and unexpected pollinator types representing novel pollination systems. Additional research may well lead to others.

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