

## Reproductive biology of an alpine orchid *Phaius delavayi*

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**Abstract** The genus *Phaius* is distributed mainly in pantropical areas, and most species reported are autogamous. In contrast, *Phaius delavayi*, an alpine plant endemic to temperate zones of China, is strictly pollinator dependent. Only female workers and males of the bumblebee species *B. hypnorum* and *B. lepidus* are effective pollinators. The pollinaria are deposited on top of the head or the prothorax of the pollinators. The different depositions of pollinaria are regarded as an adaptation of the chamber dimensions of the flower to the size of the pollinator. The natural fruit set reported here (24.6–37.1%) suggests that pollination is successful in the deceptive *P. delavayi*. The yellow perianth and sweet floral scent of *P. delavayi* are important cues in attracting pollinators, while flowering time and mass population are associated with the process of “learning and avoidance” of the rewardless flowers. This orchid, therefore, employs a deceptive pollination strategy with diverse pollinators and pollinaria depositions rather than autogamy as do its congeners.

**Keywords** Breeding system · Deceptive pollination · Functional morphology · *Phaius delavayi* · Pollinaria deposition

### Introduction

The Orchidaceae are renowned for their spectacular floral structures ensuring cross-pollination (Darwin 1890; van der Pijl and Dodson 1966; Dressler 1993). Most orchids require an external pollinating agent, but autogamy is fairly common within the family (Dressler 1993; Tremblay et al. 2005). Van der Pijl and Dodson (1966) estimate the occurrence of autogamy to be about 3%, and Catling (1990) suggests that autogamous pollinations occur in some 5–20% species of the Orchidaceae. The subtribe Blettiinae of the subfamily Epidendroideae seems to be especially dominated by autogamy. It has about 21 genera and 400 species with a distribution mainly in pantropical areas and extending into temperate Asia and North America (Dressler 1993). The breeding systems of 30 out of 400 species have been reported, and two-thirds are autogamous (van der Cingel 2001).

*Calanthe* and *Phaius* are two closely related genera in Blettiinae (Dressler 1993). The genus *Phaius* includes about 40 species with distributions in tropical Africa, tropical and subtropical Asia and Oceania (Dressler 1993). *Calanthe*, with about 150 species, is distributed in tropical and subtropical Asia the Pacific area (Tsi 1999). *Calanthe* differs from *Phaius* by a short labellum, which is fused with the column, the long pollinia with stipes and the single viscidium (Perner and Cribb 2002). Based on floral syndromes, *Calanthe* is thought to be pollinated by Lepidoptera, while *Phaius* is bee pollinated (Dressler 1993). Lepidopteran pollination has been confirmed in *C. triplicata* (Sugiura

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and Miyanaga 1996), but pollination by large bees is reported in *C. sieboldii* (Sugiura et al. 1998). Seven other *Calanthe* species are autogamous (Catling 1990). For *Phaius*, only the widespread species *P. tankervilleae* (distributed in tropical and subtropical Asia and Australia) is bee pollinated (van der Pijl and Dodson 1966), but auto-pollination and cleistogamy have also been reported (Gandawidjaja and Arditti 1982; van der Cingel 2001). Seven other *Phaius* species are described as autogamous (Catling 1990; van der Cingel 2001).

Autogamous flowers of *P. tankervilleae* do not open fully. Their pollinarium drops onto the stigma while flowers are still in the bud stage (cleistogamy) or when the perianth segments start to separate (Gandawidjaja and Arditti 1982). In contrast, insect pollination of the allogamous *P. tankervilleae* resembles the mechanism described for *Cattleya* (Darwin 1890). In *P. pictus*, an Australian species, the upper margins of the stigma expand and engulf the pollen after early anther movement (Jones 1976).

*Phaius delavayi* (Finet) P. J. Cribb et Perner (= *Calanthe delavayi* Finet) is endemic to temperate, southwestern China at elevations of 2,700–3,450 m (Tsi 1999; Perner and Cribb 2002). Although its generic placement has been disputed (Perner and Cribb 2002), *P. delavayi* is the temperate, alpine representative species of a predominantly tropical and self-pollinating orchid genus. Considering that there is a common trend of pollinator scarcity in high mountains (Kearns and Inouye 1994; Bingham 1998; Totland 2001; Bliomis and Vokou 2001) and that this may exert selective pressure via pollinator limitation promoting the evolution of self-pollination as a reproductive assurance mechanism (Galen 1985; Miller et al. 1994; Totland 2001), the reproductive biology of *P. delavayi* becomes an interesting problem. In this study, we investigate the breeding system of *P. delavayi* and its pollination ecology. The following questions are addressed: (1) What kind of breeding system does it have? (2) If it is autogamous, is the self-pollination mechanism of *P. delavayi* similar to that of its congeners? (3) If *P. delavayi* is entogamous, what kind of pollination strategy is employed? (4) What are the probable causes for its not employing autogamy as do its congeners? and (5) How does it overcome pollinator scarcity in alpine mountains?

## Materials and methods

Studies were conducted in the Huanglong Valley, Huanglong Nature Reserve, Sichuan, China. Thousands of plants of *Phaius delavayi* thrive in open scrub or on grassy slopes of the valley at elevations of 3,100–3,400 m (Li et al. 2005).

## Pollination observation

Pollination observations were made over a total of 64 h in 2005 and 2006. Some clumps with 20–40 blooming plants were chosen for observation, which was conducted only on sunny days. The behaviour of visiting insects was recorded from the moment they approached the flowers until they left. The insects' activities, especially those of pollinators, including approaching, landing on and entering the labellum, were recorded using a tape recorder. Insect visitors were captured and killed in a jar using ethyl acetate fumes. These specimens were identified by H. L. Xu of the Chinese Agriculture University and deposited at the Chinese National Herbarium (PE), Institute of Botany, Chinese Academy of Sciences.

## Floral functional morphology

As the size of the chamber is the most probable key to pollination success, we examined the morphological relationship between the floral traits and the important insect visitors. Twenty fresh flowers from 15 plants were chosen at random for morphological measurements. The length, width and height of the labellum chamber and the spur length were measured in a whole flower (Fig. 1b). The distance between the anther and the bottom of the labellum was measured in longitudinally sectioned flowers to the closest 0.1 mm (Fig. 1c) using digital calipers. The distance from the stigma to the base of the labellum was not measured, because the stigma is concave and lies behind the anther, which makes exact measurement difficult. The body length, width, thorax height, head height and proboscis length of the sampled bumblebees (queens, workers and males) were also measured to the closest 0.1 mm.

## Breeding systems

Four experiments were conducted in 2005 to test the breeding system of *Phaius delavayi*. In each experiment, 20 flowers were chosen at random on their first day of anthesis. After the labellae were removed to exclude insect pollination, the following manual pollination trials were carried out: (1) cross-pollination by using pollinaria from donor plants that grew at least 3 m away from the plants under investigation, (2) self-pollination (geitonogamy) by using pollinaria of another flower on the same inflorescence, (3) artificial self-pollination (autogamy) by directly transferring the pollinaria onto the stigma of the same flower and (4) spontaneous self-pollination (mechanical autogamy). The fruit set of the experimental series as well as that of untreated flowers was recorded in August.



**Fig. 1** Flowers and pollinators of *Phaius delavayi* in Huanglong Valley, Sichuan, China. All photos taken under natural field conditions. Scale bars = 1 cm. **a** One natural clump of *P. delavayi*; **b** close-up view of an inflorescence of *P. delavayi*. LL length of the labellum chamber; WL width of the labellum chamber; HL height of

the labellum chamber; **c** longitudinal section of the labellum of *P. delavayi*. AL distance from the anther to the bottom of the labellum; **d** *Bombus* sp. in the labellum of *P. delavayi*; **e** *Bombus* sp. taking the pollinaria on its vertex; **f** *Bombus* sp. taking the pollinaria on its prothorax

## Results

### Floral presentation

The plant of *P. delavayi* can reach a height of 30 cm (Fig. 1a). The raceme bears one to seven, but usually three to five, flowers (Fig. 1b). The flowers are yellow with red markers on the labellum (Fig. 1b). The labellum is obovate with three ridges on its upper surface. The two lateral lobes of the labellum are incurved and embrace the column, forming a chamber (Fig. 1c). At the base of the labellum, there is a straight spur, 0.6–1.0 cm in length and 0.15 cm in diameter. The anther terminates the column, and eight pollinia are borne under the anther cap. The rostellum is a broad, quadrate projection, and the viscid stigma lobes lie beneath the rostellum. The flowers have no perceptible nectar, but emit a faint sweet scent detectable by human olfaction.

Flowers of *P. delavayi* bloom in June–July, overlapping with the flowering of *Berberis polyantha* and *Rosa*

*omeiensis*, *Pedicularis recurva*, *Pedicularis torta*, *Polygonum sphaerostachyum* and *Pyrola* spp. Sympatric orchid species, including *Cypripedium tibeticum*, *C. flavum*, *Ponerorchis chusua* and *Galearis diantha*, also bloomed during this period.

### Flower visitors and their behaviour

Flowers of *P. delavayi* attracted 11 insect species belonging to eight families of three orders: Hymenoptera, Diptera and Coleoptera (Table 1). *Bombus hypnorum*, *B. lepidus*, *Formica* sp., *Baccha elongae* and *Poletes orientalis* were observed entering the labellum chamber. However, only female workers and males of the bumblebee species *B. hypnorum* and *B. lepidus* carried the pollinaria. According to our observations, these two species were similar in behaviour when they visited the flowers.

During the 64 h of observation, we observed that bumblebees landed 19 times on the inflorescences of *P. delavayi*. Among them, on 16 occasions the bumblebees

**Table 1** Insects recorded as flower visitors of *Phaius delavayi*

Order and family	Species
Hymenoptera	
Apidae	<i>Bombus hypnorum</i> * <i>Bombus lepidus</i> *
Halictidae	<i>Lasioglossum subopatum</i>
Formicidae	<i>Formica</i> sp.*
Diptera	
Syrphidae	<i>Baccha elongae</i> * <i>Rhingia campestris</i>
Culicidae	<i>Platosciara</i> sp.
Calliphoridae	<i>Calliphora vomitoria</i>
Anthomyiidae	<i>Delia unguitigris</i> <i>Polietes orientalis</i> *
Coleoptera	
Elateridae	<i>Agrypnus</i> sp.

\* Insects found in the labellum chamber

crawled into the labellum chamber and 12 times carried away pollinaria when exiting the flower. Except for once, the bumblebees landed first on the sepals, petals or labellum, and then moved toward the entrance of the labellum chamber. Once, we recorded the bumblebee flying away after losing its grip on the labellum of the pendant flower. Once, we found that a queen was too large to enter the labellum chamber, although she tried to do so repeatedly. The length of time a bumblebee remained in the chamber (Fig. 1d) varied from 2 to 30 s [mean 14.3 s, standard deviation (SD) = 5.7 s,  $n = 16$ ]. After backing out, 15 bumblebees flew away immediately, while 4 of them climbed up to the labellum for a brief rest.

The bumblebees usually visited only one flower on an inflorescence, and then left the site ( $n = 13$ ). We observed, however, four bumblebees that continuously visited two flowers of one inflorescence, and two bumblebees visiting two separate inflorescences in succession. We could not observe whether bumblebees entered the labellum bearing pollinaria or not from a long distance

because they were flying too fast. We found on 12 occasions that the pollinia of *P. delavayi* were stuck to the broad, shallow and highly viscid stigmatic surface after the bumblebee left the flower.

Seven collected bumblebees were found bearing pollinaria of *P. delavayi*. Five worker bumblebees carried pollinaria on their vertex (top of the head; Fig. 1e). One worker carried the pollinaria on the front edge of the thorax (pronotum; Fig. 1f). One male bumblebee carried the pollinaria on its vertex. For the number of pollinaria on the bumblebees, four bumblebees (three females, one male) had 2 pollinaria, two workers had 4 and one worker had 16.

#### Parameters of floral morphology versus bee dimensions

Queen bumblebees were generally larger than workers and males (Table 2). The average spur length of the flowers was shorter than the average proboscis length of all the bumblebees measured. The width (WL) and height (HL) of the labellum chamber were apparently smaller than the body width and thorax height of the queen bumblebees, so the queens were unable to enter the chamber.

In contrast, the WL and HL of flower were comparable to the body width and thorax height of the workers, and larger than those of the male bees. In most cases, the length of the workers and the male bees was less than that of the labellum chamber (LL). These bees could enter the labellum chamber to probe the flower's spur (Fig. 1d). The distance from the anther to the base of the labellum (AL) was apparently lower than the thorax height of workers and males, but it was comparable to the height of the heads of these bees.

When smaller bees entered the labellum chamber, their heads were too low to contact the anther and instead the anthers contacted the bees' prothorax just behind the head (Fig. 1f). For example, the head of a small worker bumblebee was 0.14 cm high and the thorax was 0.37 cm high, which was smaller than most of the bumblebee specimens we collected. It carried the pollinaria on the prothorax rather than on the head.

**Table 2** Floral functional architectures of *Phaius delavayi* and body size of bumblebees

Floral architecture	Size (cm) (mean $\pm$ SD)	Queen bumblebees	Worker bumblebees	Male bumblebees	Size (cm) (mean $\pm$ SD)
LL	1.62 $\pm$ 0.19	1.99 $\pm$ 0.23	1.43 $\pm$ 0.21	1.19 $\pm$ 0.09	Body length
WL	0.62 $\pm$ 0.08	0.90 $\pm$ 0.11	0.62 $\pm$ 0.08	0.55 $\pm$ 0.03	Body width
HL	0.50 $\pm$ 0.07	0.71 $\pm$ 0.06	0.51 $\pm$ 0.08	0.39 $\pm$ 0.02	Thorax height
AL	0.17 $\pm$ 0.03	0.32 $\pm$ 0.02	0.22 $\pm$ 0.02	0.17 $\pm$ 0.03	Head height
LS	0.95 $\pm$ 0.13	1.57 $\pm$ 0.01	1.10 $\pm$ 0.22	0.97 $\pm$ 0.02	Proboscis length

The results of floral traits are taken from 20 flowers; queen bumblebee sizes are taken from 4 individuals, workers from 17 and males from 3 individuals

LL length of the labellum chamber; WL width of the labellum chamber; HL height of the labellum chamber; AL distance from the anther to the bottom of the labellum; LS length of the spur

**Table 3** Breeding system and fruit set of *Phaius delavayi*

Treatment	No. of flowers	No. of capsules	Fruit set (%)
Cross-pollination	20	20	100
Self-pollination	20	19	95
Hand geitonogamy	20	20	100
Spontaneous self-pollination	20	0	0
Natural pollination (2005)	8,863	2,184	24.6
Natural pollination (2006)	1,850	686	37.1

Whenever worker or male bumblebees carrying pollinaria on their bodies entered the labellum, some or all of the pollinaria were caught by the viscid stigma.

#### Breeding system

Natural fruit set was 24.6% ( $n = 8,863$ ) in 2005 and 37.1% ( $n = 1,850$ ) in 2006. Both manual cross-pollination and self-pollination via geitonogamy resulted in 100% fruit set. Manual autogamy produced 95% fruit set (Table 3). The difference between natural pollination and hand pollination was significant ( $\chi^2$  test,  $P < 0.01$ ). Control flowers that had the labellum removed but were not manually pollinated set no fruit.

#### Discussion

##### The breeding system of *Phaius delavayi*

Fruit set following pollination experiments indicate that flowers of *P. delavayi* are strictly entomophilous. For autogamous flowers of *Phaius*, their pollinaria drop onto the stigma or the stigma expands and engulfs the pollinaria (Jones 1976; Gandawidjaja and Arditti 1982). In contrast, *P. delavayi* possesses typical floral features favouring cross-pollination. It has fully open flowers. The pendent flower makes the column horizontal and places the stigma and anther on the same level. This prevents the pollinaria from falling onto the stigma after both the rostellum and anther cap have withered.

Tremblay et al. (2005) showed recently that deceptively pollinated orchid species have, in general, about half the percentage fruit set of rewarding species (i.e.  $20.7 \pm 1.7\%$ ,  $n = 130$  versus  $37.1 \pm 3.2\%$ ,  $n = 84$ ). The natural fruit set reported here (24.64–37.08%) (Table 3) indicates that pollination is successful in the rewardless *P. delavayi*. This can be interpreted as being for two reasons. One is that both medium-sized and small bumblebees (Table 2) could be effective pollinators of *P. delavayi*, increasing the chance of pollination. The second is that pollinators are not scarce in the habitat of *P. delavayi*. Although the literature suggests a common trend of pollinator scarcity in high

mountains (Kearns and Inouye 1994; Bingham 1998; Totland 2001; Bliomis and Vokou 2001), approximately 15 large bumblebee colonies nest in the 3.6-km-long Huang-long Valley (Ran, unpublished data), and these bumblebees are active in the warmest month (July) when the flowers of *P. delavayi* are in bloom. Self-pollination is evolved mainly to ensure reproductive success when conditions for outcrossing are unfavourable because of an absence of mates or pollinators (Stebbins 1970). There is, therefore, no trend toward mechanical autogamy in *P. delavayi* under a regime of sufficient pollinators.

##### The special pollination system of *Phaius delavayi*

It is unusual that the same pollen vectors receive pollinaria on two different positions. The pollinators of the orchid species *Holcoglossum rupestre*, a beetle (*Hybovalgus biculatus*), pollinate the flowers in two different manners and, correspondingly, carry the pollinaria in two different positions (Jin et al. 2005). In the case of *P. delavayi*, the pollinators have similar behaviour but different sizes; smaller bees will enter deeper than larger bees into the labellum chamber. So, smaller bees will carry the pollinaria on a position behind that of larger bees when they withdraw from the flower. Thus, the different pollinaria depositions result from insect dimensions in relation to labellum chamber dimensions.

When the same vector pollinates more than one species of orchid simultaneously, different placement of interspecific pollinaria prevents any possible interference or improper pollen transfer (Dressler 1993). Maad and Nilsson (2004) showed an evolutionary shift in relation to the placement of pollinaria on the same pollinators (also in relation to the varying lengths of their probosces), leading to disruptive selection. *Phaius delavayi* is pollinated by both worker and male *Bombus* spp. that are of the right size to enter the flower, whereas bee queens are too large and are thus excluded as potential pollinators. We hypothesize that the selective pressure on the functional morphology of the labellum is exerted by the worker bumblebees, as is suggested by the close association between the chamber's size and the worker's dimensions, and because there are many more of the larger workers in the bumblebee society

than the smaller males. The different placement of the pollinaria on the functional pollinators, which vary in size relative to the flower's dimensions, serves as indirect evidence that the flowers can use all these vectors as pollinators while excluding large queens.

#### The pollination syndrome of *Phaius delavayi*

Generally, honeybees and bumblebees are regarded as locating flowers by visual cues and to orient during landing by floral fragrance cues (Dobson et al. 1999). Sugiura et al. (1998) concluded that the yellow perianth and the faint sweet floral scent probably attract bees to *Calanthe sieboldii*. Similarly, the yellow colour of *P. delavayi* is probably attractive to bumblebees, because most bumblebees show a significant preference for yellow and blue over other colours (Simonds and Plowright 2004; Heuschen et al. 2005). The primary and most common signaling function of entomophilous flowers is advertisement of pollen reward, in which the dominant yellow colour is presumed to be a mimic of pollen source (Osche 1983). Lunau et al. (1996), following this line, have shown the importance of yellow colour in attracting bumblebees in a context of feeding behaviour and pollination.

Bumblebees prefer flowers with scent (Schmitt and Bertsch 1990; Schmitt et al. 1991; Proctor et al. 1996). Although there are few data on the effects of odour compounds on bumblebee foraging, the presence of scent may enhance colour discrimination (Kunze and Gumbert 2001), and the sweet scent of the flowers of *P. delavayi* probably plays an important role in attracting bumblebees. Of course, multicomponent floral signals elicit selective foraging in bumblebees (Gegear 2005). In any event, the pollination syndrome of *P. delavayi* appears to be a generalized form of food deception.

In non-rewarding species, learned avoidance by pollinators would be expected. Pollinators will visit just a few non-rewarding flowers before switching to alternative species (Dafni 1981; Dressler 1993). This often results in low pollinator visitation and consequently low reproductive success in orchids (Dafni and Ivri 1979; Gill 1989; Neiland and Wilcock 1998). Tremblay et al. (2005) showed recently that deceptively pollinated orchid species generally have about half the percentage fruit set of rewarding species (i.e.  $20.7 \pm 1.7\%$ ,  $n = 130$  versus  $37.1 \pm 3.2\%$ ,  $n = 84$ ). The natural fruit set reported here (24.64–37.08%) indicates that pollination is successful in the rewardless *P. delavayi*. Although we do not have direct observations on the frequency of pollinator visits, the comparatively high fruit set suggests relatively high pollination efficiency even under these nectarless constraints. In other “mass and early-flowering” food-deceptive flowers, queens of *Bombus* are usually the only pollinators (Nilsson 1981). In *P. delavayi*, workers

and males are available throughout the season and ensure that pollination by deceit is not limited to the beginning of the season when the queens emerge.

In cases of general food-deceptive species which appear in large populations (e.g. *Dactylorhiza* sp. Nilsson 1980), orchid flowers open at the beginning of the flowering season, before other rewarding species, to deceive naïve bumblebees. One would expect that large populations of deceptive species would reduce their individual pollination success because of density-dependent negative selection via the process of learning and avoidance of the non-rewarding flowers (Smith and Gigord 2001). However, the flowers of *P. delavayi* bloom in July, when bumblebees are active in the warmest month of an austere cold habitat. So, even if a process of “learning and avoidance” exists (due to the deceptive plant's high density as well as the existence of scent) and may reduce the visitation rate, the high number of potential pollinators will be able to compensate for any possible avoidance.

The case of *P. delavayi* thus exemplifies a unique situation in the genus *Phaius*: It is a strictly entomogamous species of a genus dominated by auto-pollination. This species appears in a large population producing odouriferous, showy flowers. Its flowering season is not limited to the beginning of the season, exploiting possibly naïve pollinators, and has relatively high reproductive success for a deceptive orchid.

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