

## Pollination of a slippery lady slipper orchid in south-west China: *Cypripedium guttatum* (Orchidaceae)

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*Cypripedium guttatum* was studied in north-west Yunnan at 3490 m a.s.l. The flowers are rewardless 'kettle traps'. The structure of the lip, where pollinators are temporarily kept prisoner, and the method of their capture, are unusual in being *Paphiopedilum*- rather than *Cypripedium*-like. The deceptive orchid does not mimic any of the diverse flowers concurrently blooming in the habitat, all being visited by the polylectic pollinators of *C. guttatum*, viz. *Lasioglossum virideglaucum*, *L. clypeinitens* and *L. sauterum*, besides two additional probable pollinators and four non-pollinating visitors (all Halictidae; three new species). The bees got caught when they tried to climb onto the staminode and their forelegs slid down its slippery downward ridges, causing them to tumble to the pouch bottom. To leave, they had to climb a tunnel leading past the stigma to the anthers where a pollen smear was acquired while extruding themselves from the narrow exit. The similarities with myiophylous *Paphiopedilum* are discussed in view of the possibility that they may foreshadow evolutionary transitions between melittophily and myiophily found in slipper orchids. © 2005 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2005, 148, 251–264.

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### INTRODUCTION

The flowers of slipper orchids are 'kettle traps' without known rewards (Delpino, 1867, 1869; Müller, 1873; Vogel, 1965; Nilsson, 1979; Bänziger, 1996). The state of knowledge on the deceptive pollination mechanism operating in *Cypripedium* has been reviewed by Stoutamire (1967) and Nilsson (1979). Unfortunately, progress has been very slow, mainly because slipper orchids are infrequently to very rarely pollinated and have become restricted to a few sites which are often difficult to access. At Kipping's time (1971), just seven of the 45 known species had their pollinators established, viz. *C. acaule* Ait., *C. arietinum* P. Br., *C. calceolus* L., *C. californicum* A. Gray, *C. candidum* H. L. Mühl. ex Willd., *C. parviflorum* Salisb., and *C. reginae* Walt. Three decades passed before an addi-

tional species joined the list, *C. macranthos* Sw. (Sugiura *et al.*, 2001).

*Cypripedium* is pollinated by various wild bees, mainly Andrenidae, Halictidae, Megachilidae and Apidae [viz. Xylocopinae, Anthophorini, Bombini (systematics after Michener, 2000)] (Müller, 1868, 1869; Guignard, 1886; Stoutamire, 1967; Daumann, 1969; Kipping, 1971; Nilsson, 1979; Catling & Knerer, 1980; Davis, 1986). Pollinators are only suspected in *C. debile* Rchb. f., possibly fungus gnats (Mycetophilidae) because it has a mushroom-like odour (Stoutamire, 1967; Vogel, 1978).

Knowledge of pollination in other slipper orchid genera is even more meagre. In the New World genera *Mexipedium* Albert and Chase and *Selenipedium* Rchb. f., both monotypic, the pollinators are unknown, while in the 15 species of *Phragmipedium* Rolfe bees as well as hoverflies (Syrphidae) have been reported (Dodson, 1966). In south and south-east Asian *Paphiopedilum* Pfitzer, with some 70 species the largest

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genus, six species have been successfully researched, all pollinated by hoverflies (Atwood, 1985; Bänziger, 1994, 1996, 2002).

Morphologically, *C. guttatum* Sw. holds a special position among *Cypripedium*. The lip does not resemble a *Cypripedium* but rather a *Paphiopedilum*. Because of this, it was of particular interest to elucidate whether its pollination syndrome is according to the former or the latter; melittophily vs. myiophily may have implications for our understanding of the evolution of slipper orchids.

*C. guttatum* is the most widely distributed slipper orchid and the only species present in both the Old and the New World. It ranges from easternmost Europe (Urals) across Siberia to Sakhalin, north-east China, Korea, Japan, and on to north-west America; it is also present in India, Nepal, Bhutan and south-west China (Sichuan, Tibet and Yunnan) (Cox *et al.*, 1997; Cribb, 1997; Chen, 1999). In eastern Asia and north-west America the closely related *C. yatabeanum* Makino is found, which some authorities consider to be a variety of the former. Yet, despite *C. guttatum*'s wide range, it has never been studied anthecologically. It is one of the smallest species, completely outshone by its gorgeous congeners.

The present study is part of a series planned to unravel the natural reproductive biology of Chinese lady slipper orchids, both for scientific interest and as a means of finding ways to improve their conservation. With some two thirds of the known *Cypripedium* species, China has the world's richest slipper orchid flora, yet ours is the first pollination study of slipper orchids in China.

## MATERIAL AND METHODS

Elevations were measured with a Thommen anaeroid (margin of error 10 m) calibrated with Zhongdian town (main central road) at 3400 m (*vide* Russian Map of China, 1 : 200 000, Yunnan Province, Zhongdian County, No. G47-IV), repeatedly measured and averaged. Temperature and humidity were read from an electronic min/max Thermo-Hygrometer (Oregon Scientific). When necessary, especially during the sensitive phase before they entered a flower, insect visitors were observed from a safe distance with a Vixen monocular (8 × 20, focusable down to 0.4 m). Once the flower-entering phase started, they were less wary and close observation was possible. Insects were caught by net or with a translucent plastic box placed over the flowers, killed with ethyl acetate, each transferred to one film canister and appropriately labelled. In the evening they were pinned and properly set, or placed between well-dried tissue papers in a tight box with thymol and naphthalene as fungicide and insecticide.

During the period from 5 and 21 June 2002 we observed *C. guttatum*, *C. flavum* P.F. Hunt & Summerhayes, *C. tibeticum* King ex Rolfe, *C. yunnanense* Franchet, and other flowers for 15 days, between 09:00 and 16:00–17:00, i.e. well before and after pollinator activity was observed. Total watching time of *C. guttatum* was 19.5 man-hours.

## THE FLOWER

### STUDY SITES

*C. guttatum* was studied mainly at Na Pa Hai, 3490 m a.s.l., about 20 km north-west of Zhongdian town, north-west Yunnan, south-west China. Temperatures were generally 17–19 °C around 09:00 (minimum 15 °C), reached 21–25 °C around 14:00 (maximum 30 °C), and returned to 19–21 °C around 16:00–17:00. The relative humidity was quite low and ranged between 35 and 57% when it did not rain. The early mornings tended to be rather cloudy; the late mornings and early afternoons were generally sunny with intermittent clouds, then often cloudy again. Only two days were rainy throughout.

### HABITAT, POPULATION STRUCTURE AND PHENOLOGY

Na Pa Hai is on a gentle north-east facing slope. It is an autumn-meadow below the alpine zone where yak (*Bos grunniens*) graze in autumn. The grazing disturbance is heavy and leads to much loss of orchid fruit, although the spring/summer flowering is not affected. *C. guttatum* plants tend to survive grazing in dense juniperus (*Sabina squamata* (Buch.-Ham.) Ant.) or juniperus-cotoneaster turfs which grow around scattered shrubs such as *Crataegus oresbia* W.W. Smith or *Berberis dictyophylla* Franchet. Other plants nearby included: *Anemone rivularis* Buch.-Ham. ex DC., *A. obtusiloba* D. Don., *Aster* sp., *Euphorbia stracheyi* Boiss., *E. yunnanensis* Radcliffe-Smith, *Heracleum candicans* Wall. ex DC. (a tall, bush-like herb), and the treelet *Rosa omeiensis* Rolfe. At the margin of this meadow there is a forest of *Pinus yunnanensis* Franchet and *Quercus pannosa* Hand.-Mazz. Three other slipper orchids were also present: *C. flavum* P.F. Hunt, *C. tibeticum* King ex Rolfe and *C. yunnanense* Franchet.

There were 22 clusters of *C. guttatum* with 11–165 flowers (total 663 flowers) spread over an area of about 1 × 0.2 km. Flower watching sessions took place at the largest cluster with 165 densely packed flowers, in a patch little more than 1 m<sup>2</sup> in area (Fig. 1). It was only very slightly inclined towards the north. The cluster was fully or partially in the shade of trees or fronds until about 13:00, after which it was in full sunshine for some 3 h. From 16:00 it was again in full shade.





**Figures 1–3.** Fig. 1. Large cluster of *Cypripedium guttatum*. Note the white sepal and pink-purple, white-mottled, pouch and petal. Fig. 2. Lateral view of a flower. Fig. 3. *Lasioglossum clypeinitens* extricating itself out of the exit of *C. guttatum*. The halictid bee has moved somewhat beyond the anther from where it has smeared off a pollen load sticking to its thorax. *Abbreviations:* a, anther; f, flap; pl, pollen load; s, staminode. All photographs by H. Bänziger.

The study period was from before peak flowering until only a few fresh flowers remained. Flower longevity is about 2 weeks. According to local orchidologists the capsules mature in 3–4 months and split open before the first snow falls in October.

#### FUNCTIONAL MORPHOLOGY

##### *Peduncle, upper sepal and petals (Figs 1–5)*

The flower stands about 10–15 cm above ground and only a little above the grass carpet. The sepal, remark-

ably dull white outside but pink-purple inside, is generally horizontally set or even downward inclined in front. In some cases it is somewhat uplifted or even reflexed. Thus, when the cluster is seen from above and some distance away, it gives the impression of an aggregation of white blotches contrasting with the meadow's green background. When seen from a lower level, the irregularly mottled, purple-pink and white lip and petals become visible. Therefore, one main function of the sepal is evidently to advertise the flower to pollinators. The other is to shelter the pouch from rain.

Near the base of the petals is a tuft of white hairs about 1 mm long. The tuft, set just above the lip's exit gap, is a functional part of the mechanism, enforcing the acquisition of pollen by the pollinator, as explained below.

#### *Lip (Figs 2–5, 11)*

The lip (pouch) is pitcher- rather than shoe-shaped and thus resembles that of *Paphiopedilum* (except the subgenus *Parvisepalum*). Also, the rim lacks the incurved flaps except at the rear. Here the flaps (f, Fig. 3) join and extend well below the staminode and half way up behind it. The flaps are shiny and slippery. As in other slippery surfaces (e.g. the pouch) in such orchids, this is most likely due to a film of fatty oil (Knoll, 1922). In *C. guttatum* the flaps' function is not that of a sliding slope for capturing pollinators, as described for *C. calceolus* (Daumann, 1969). Rather, they have two other purposes. On the inside, they form part of the tunnel leading the pollinator to the exits. On the outside, their slippery surface prevents a captured pollinator from climbing up and escaping through the entrance.

Near its rim, the pouch is slightly everted at the front. A translucent 'window' is below each anther. On the inside, the front wall of the lip is slightly overhanging due to the natural inclination of the flower, while the back wall is inclined at c. 30° near the bottom, becoming increasingly steep and overhanging near the top. The wall is slippery and glabrous except on a central, hair-studded band 2–3 mm wide extending from the bottom to the pouch's two exits. The hairs are white, up to 1 mm long, and more or less upwardly inclined, so that they can be used by the pollinators to climb the wall. In addition, opposite the stigma and at the exit gap, the hairs also function as an elastic mat that keeps the pollinator pressed against the stigma and anthers as it climbs towards the exit.

*Staminode, stigma, anthers and pollen (Figs 2, 3, 6–9)*  
The tongue-shaped staminode is strongly curved downwards and longitudinally intersected by ridges and furrows (rf, Fig. 7) which are shiny and slippery. It has a role similar to that of *Paphiopedilum*,

but the working details are different, as explained below.

The stigma faces the hair-studded back wall of the pouch. The distance between the papillose stigmatic surface and the wall is adjustable to some degree to accommodate variation in size of the pollinator and adequately to force their back against the stigma to sweep off pollen (if present). Namely, the clearance can be widened by deflecting the pouch downward since it is elastically hinged to the ovary.

The two anthers, facing backward and somewhat downward as in other *Cypripedium*, not upward and somewhat backward as in *P. villosum*, are flexibly attached. Thus, as the pollinator negotiates the exit, it deflects the anther into an upward position, an action which forcefully presses the pollen to stick to the back of the thorax. The exit of the pouch, being set somewhat higher than the anther, forces the exiting pollinator to bend itself backwards and leave in a somewhat supine position (Figs 3, 14). The clearance of the exit is slightly less than 1 mm when measured from the pollen surface to the tip of the hairs at the gap and petal base. However, when the hairs are bent by the pollinator, the gap increases to 1.5 mm or slightly more. Hence the effective working clearance is elastically adaptable, one of three mechanisms ensuring that the pollinator is pressed against the anther (the other two being the deflectable anthers and the backward bending of the pollinator).

The pollen is presented as a sticky, amorphous mass of pale yellow colour. On the black thorax of halictid bees it is readily recognizable as such, even on an air-borne (hovering) vector.

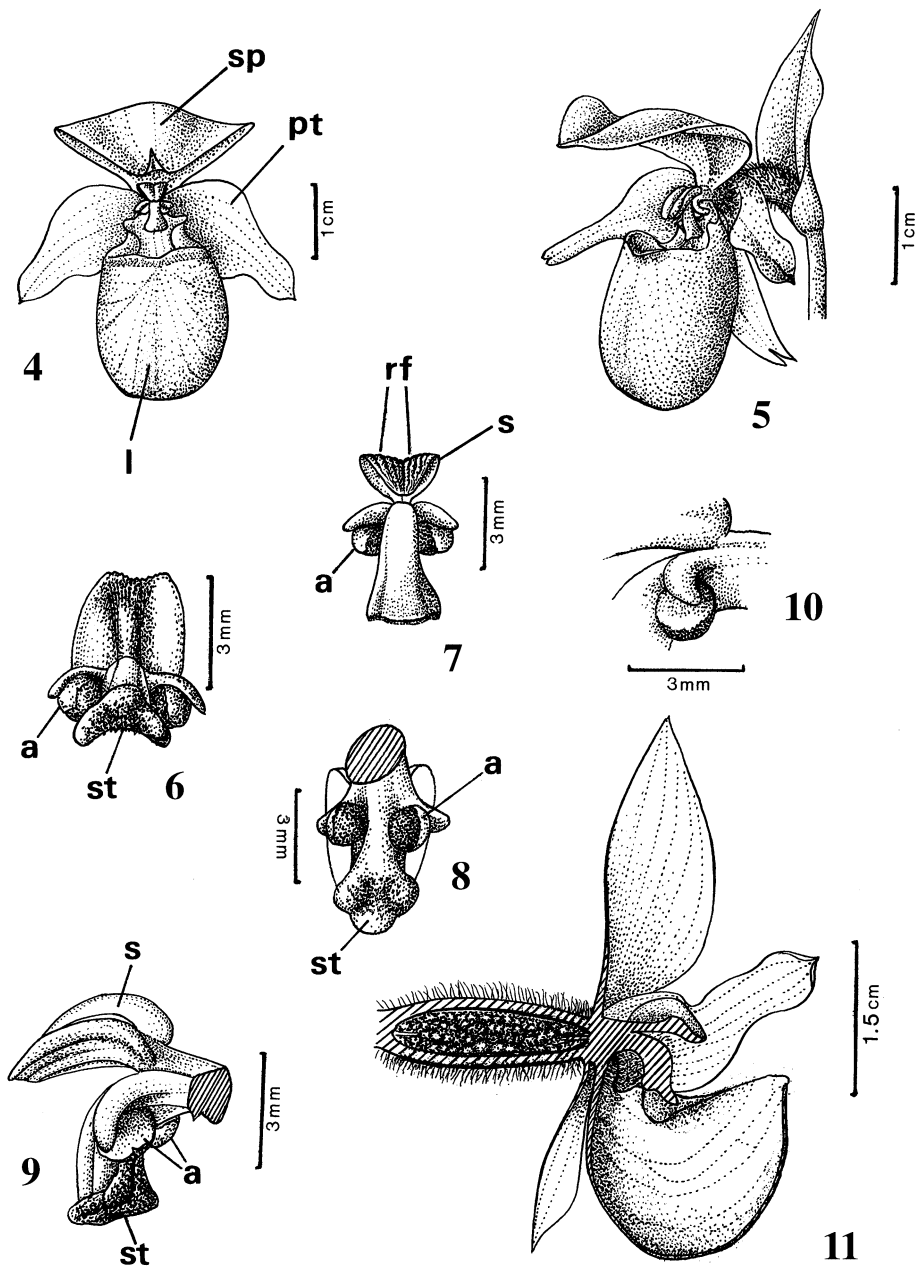
#### *Odour emitted*

The scent is fragrant and different from the other *Cypripedium* species at the site. The scent of a single flower is weak and perceptible only by close smelling, but the assemblage of many dozens of flowers sometimes makes it perceivable at 0.5 m away. As in *P. villosum*, the scent tends to become perceptible after direct sunlight has reached the flowers. Higher temperature probably increases the emission of the scent.

## THE FLOWER VISITORS

Although only species of Halictidae were found to pollinate *C. guttatum*, other visitors of this and other slipper orchids are treated in detail. This is to explain better why only some of the visitors are pollinators of *C. guttatum*. This broad approach adds indirect evidence that the species found to be carrying pollen are the actual, legal pollinators, despite the (statistically) few events seen.





**Figures 4–11.** Morphology of the flower of *Cypripedium guttatum*. Figs 4, 5. Frontal and semilateral view of whole flower. Figs 6–9. Column in dorsal, frontal, basal and lateral views, respectively. Fig. 10. Position of anthers. Fig. 11. Longitudinal cross-section of flower through the column. Abbreviations: a, anther; l, lip; rf, ridges and furrows; pt, petal; s, staminode; sp, sepal; st, stigma. Drawing by Sun Yin-bao.

The hymenopterous attendance was very low on all flowers, throughout the area and study period. Only 86 specimens of Halictidae were collected from *Cypripedium* and non-*Cypripedium* flowers, and less than half as many of the other bee families combined (Apidae, Andrenidae, Colletidae, Megachilidae). An additional, unknown number of halictids was observed on various flowers near, and on, *C. guttatum*; they were

not taken in order to increase the chances of seeing pollination events.

**THE POLLINATORS OF *C. GUTTATUM*, HALICTID BEES**  
The Halictidae (sweat bees) is a very difficult group taxonomically. Over 3400 species are known; they are spread worldwide. The vast majority are polylectic

(e.g. Westrich, 1989). In spring and early summer, only female adults are on the wing, the males appearing later on (A. Ebmer, pers. comm.), as also found in our study. According to Michener (2000), all gradations from ordinary solitary life to communal or eusocial behaviour with clearly recognizable queen and worker castes have been found. Nests are made in burrows in banks or level soil. Some species (e.g. *Sphecodes* spp.) exhibit cleptoparasitism or social parasitism.

Ten halictid species belonging to three genera were found (Table 1). Their visits to the various flower species are summarized in Tables 2–5. All halictid specimens collected were females except one *Sphecodes* sp. near *hyalinatus*. Three species, viz. *Lasioglossum clypeinitens* Ebmer, *L. flavohirtum* Ebmer and *L. mystaphium* Ebmer, were new to science at the time of our field study. Seven specimens of *L. virideglaucum*, one of *L. clypeinitens* and

**Table 1.** Halictidae collected in the study area and their dimensions. *Lasioglossum* spp. are listed in order of size. All are females except one *Sphecodes* sp. nr. *hyalinatus*. \*Species new to science at the time of the study (Ebmer, 2002)

	No. specimens	Thorax height (mm)	Total body length (mm)
Smallest			
<i>L. mystaphium</i> * Ebmer	2	1.1	5.4–5.6 (x = 5.5)
Small			
<i>L. sauterum</i> Fan & Ebmer	1	1.3	6.0
<i>L. virideglaucum</i> Ebmer & Sakagami	23	1.4–1.6 (x = 1.5)	6.0–7.4 (x = 6.7)
<i>L. allodalum</i> Ebmer & Sakagami	3	1.4–1.6 (x = 1.5)	6.9
<i>L. clypeinitens</i> * Ebmer	11	1.5–1.8 (x = 1.7)	6.8–7.5 (x = 7.1)
Medium			
<i>L. excisum</i> Ebmer	13	2.0–2.3 (x = 2.1)	8.7–9.6 (x = 9.2)
<i>L. flavohirtum</i> * Ebmer	8	2.1–2.3 (x = 2.2)	8.7–9.9 (x = 9.5)
Large			
<i>L. zonulum euronotum</i> Ebmer	20	2.5–3.1 (x = 2.8)	9.4–11.3 (x = 10.4)
Non- <i>Lasioglossum</i> taxa			
<i>Sphecodes</i> sp. nr. <i>hyalinatus</i> Hagens	3	1.6–2.1 (x = 1.9)	7.8–8.7 (x = 8.2)
<i>Halictus yunnanicus</i> Pesenko & Wu	1	2.2	8.3

**Table 2.** Halictid bees on various flowers (except *Cypripedium* spp.)

	<i>Anemone obtusiloba</i> D. Don (Ranunculaceae)	<i>Anemone rivularis</i> Buch.-Ham. (Ranunculaceae)	<i>Crataegus oresbia</i> W.W. Smith (Rosaceae)	<i>Potentilla fruticosa</i> L. (Rosaceae)	<i>Rosa omeiensis</i> Rolfe (Rosaceae)	<i>Euphorbia stracheyi</i> Boiss. (Euphorbiaceae)
<i>L. mystaphium</i>	1					
<i>L. virideglaucum</i>			1		2	6
<i>L. allodalum</i>					1	
<i>L. clypeinitens</i>			1			
<i>L. excisum</i>	1				3	1
<i>L. flavohirtum</i>				1	1	
<i>L. zonulum euronotum</i>	2	4	2		3	7
<i>Sphecodes</i> sp. nr. <i>hyalinatus</i>		1			1	1
Probably <i>L. clypeinitens</i> or <i>L. virideglaucum</i>	6	5	3	1	9	1
Probably <i>L. excisum</i> or <i>L. flavohirtum</i>	1	1	3			
Probably <i>L. zonulum euronotum</i>	1	1	1	1	1	

Additional records: *L. sauterum* collected only once from *Cypripedium guttatum*; *Halictus yunnanicus* collected on the wing.

Table 2. Continued

	<i>Aster</i> sp. (Compositae)	<i>Ligularia dictyoneura</i> (Franch.) Hand.-Mazz. (Compositae)	<i>Taraxacum dasypodium</i> V. Soest (Compositae)	<i>Polygonum macrophyllum</i> D. Don (Polygonaceae)	<i>Salvia brachyloma</i> Ku. (Labiatae)	<i>Heracleum candicans</i> Wall. ex DC. (Umbelliferae)
<i>L. mystaphium</i>						
<i>L. virideglaucum</i>			2			2
<i>L. allodalum</i>						
<i>L. clypeinitens</i>				1		
<i>L. excisum</i>						
<i>L. flavohirtum</i>					2	
<i>L. zonulum euronotum</i>	3	1			1	2
<i>Sphcodes</i> sp. nr. <i>hyalinatus</i>						
Probably <i>L. clypeinitens</i> or <i>L. virideglaucum</i>	1			1	1	1
Probably <i>L. excisum</i> or <i>L. flavohirtum</i>	2				1	
Probably <i>L. zonulum euronotum</i>						

*L. sauterum*, and two of unidentified *Lasioglossum* (probably *virideglaucum* or *clypeinitens*) acquired a pollen smear of *C. guttatum*. Pollen failed to be acquired by one *L. clypeinitens* and one *L. mystaphium* only because it had already been swept off by a previous pollinator. One *L. clypeinitens* was helped out by forceps after 46 min of unsuccessful attempts to leave (it had become too weak and we decided to collect it for identification).

BEHAVIOUR OF POLLINATORS ON AND IN *C. GUTTATUM*  
(TABLES 3, 4; FIGS 3, 12–15)

The period with the highest frequency of halictids arriving at the flowers was 13:00–15:00 on 7 and 8 June: a specimen flew in every 2–10 min. At other times the interval was between 30 and 60 min. After this date very little or no pollinator activity was observed, probably because they learned to avoid the rewardless orchid and because of the rapidly dwindling anthetic flowers.

We assume that from a distance of many metres the bees were alerted mainly by the white sepals contrasting against the green background, though scent may also have played a role. Generally, when near to or within a cluster of flowers, they tended to exhibit a serpentine flight course, sometimes nearly zig-zagging. This indicates that they were being guided by scent. They often hovered for a moment in front of a flower before landing. They settled on the pouch, upper sepal, or petals, in that order of frequency, but then they always proceeded to the rim of the pouch.

Soon they sneaked in between the sepal and the pouch of those flowers where the sepal was closely covering the petal. Hence they were partly out of view (to follow the events better, the observer had to crouch down to the level of the flower and peep through the gap between sepal and pouch). Next, from the rim the bee attempted to bridge the hollow past of the pouch by trying to climb onto the staminode, but the claws of the forelegs slid down its slippery, downward orientated ridges which worked like railings increasingly insecure further down. Thus, while the hindlegs initially managed to hold onto the rim, the bee was thrown off balance, causing the hindlegs in turn to lose their grip, leading to the bee tumbling to the bottom of the pouch.

Attempts to escape via the entrance by frantically trying to climb the overhanging front and lateral walls (Fig. 12) rarely succeeded, nor did wing action work due to the narrow pouch. After a minute or so the bee calmed down somewhat and started to climb the hind wall (Fig. 13), possibly induced by light suffusing through the ‘windows’ and exits. After passing the stigma (onto which pollen, if any is present, is smeared off the thorax), the bee’s head would soon appear at an anther below an exit. Here progress became very slow, except when the bee was rather smaller than average, or the pollen had already been swept off by a previous pollinator. Vibration by buzzing, which was often faintly heard, evidently helped its progress. Negotiating the gap with concomitant pollen acquisition (Figs 3, 14) (the mechanisms involved are described in ‘Functional morphology’,

**Table 3.** Behaviour of pollinators on and in flowers of *Cypripedium guttatum*. 1. Landing and subsequent behaviour. 2. Behaviour on staminode. 3. Behaviour in pouch. 4. Time to exit (minutes). 5. Pollen acquisition

	<i>L. virideglaucum</i>	<i>L. clypeinitens</i>	<i>L. sauterum</i>	<i>Lasioglossum</i> probably <i>mystaphium</i> <sup>1</sup>	<i>Lasioglossum</i> spp. <sup>2</sup>
1.	One landed on pouch, one landed on petal, then climbed to rim of pouch, then both and two additional bees advanced below the sepal. Three additional bees not seen how landed.	One landed on petal then climbed to pouch rim and advanced below sepal. Two not seen where landed.	One landed on sepal and advanced below it.	One not seen where landed but seen to advance below sepal.	Two not seen where landed but one advanced below sepal, the other not seen doing so.
2.	Three climbed onto staminode, slipped and fell into pouch. One seen falling only. Three not seen how fallen into pouch.	One climbed onto staminode, slipped but remained hanging supine on staminode bottom for a few seconds, then fell. Two not seen falling.	Not seen.	Not seen.	One climbed staminode, slipped and fell into pouch. One not seen.
3.	Four advanced 2–3 times up tunnel to anthers but backed down, possibly causing selfing. Three not seen how behaved.	Two advanced 2–3 times up tunnel to anthers, but backed down, causing selfing. <sup>3</sup> One constantly trying to leave by entrance.	Not seen.	Not seen.	One advanced up tunnel to anthers but then retreated, possibly causing selfing; one not seen.
4.	1, 1.5, 2, 2, 4, 6, 14	4, 14, 46 <sup>4</sup>	8	1	3, 7.
5.	In all 7	In one; one was extracted out of pouch by hand; one no pollen acquired because already exhausted by previous pollinator.	In one	Probably none as exited very rapidly, pollen possibly exhausted.	In both.

<sup>1</sup>Escaped. Identification based on the fact that this bee was very small and exited very quickly, as would be expected by *L. mystaphium* present in the area.

<sup>2</sup>Escaped, but photographed on leaving the exit. Probably *L. virideglaucum* or *L. clypeinitens*.

<sup>3</sup>Retreated down into pouch with pollen on back, climbed up again and was seen near exit without the pollen, evidently after having smeared it off onto the stigma, causing selfing.

<sup>4</sup>Helped manually to come out after 46 min.



above) was the slowest part of the process, requiring 1–4 min.

However, in many cases the advancing proved so difficult that the bee backed down, sometimes into the bottom of the pouch, and the whole sequence restarted. Generally, this backing down occurred before a smear was acquired, but occasionally the bee retreated from a very advanced position where it had already acquired a pollen load. Thus self-pollination occurred, observed at least twice with *L. clypeinitens*. Normally, this may not occur as often; it is possible that the bees were scared by our presence and retreated.

After the bee exited the gap, it mostly flew off in a moment, but sometimes it climbed the sepal (Fig. 15)

**Table 4.** Additional observations on pollinators of *Cypridium guttatum*

<i>L. virideglaucum</i> or <i>L. clypeinitens</i>	Two flew near <i>C. guttatum</i> , one of which had a pollen smear typical of <i>C. guttatum</i> . One hovered in front of flower but was blown off by strong wind. One advanced below the sepal but then flew off. One landed on grassy ground 0.5 m from flowers, possibly to enter its nest.
Probably <i>L. mystaphium</i>	Landed on sepal, flew off after 2 min

and tried to sweep off the pollen with its legs – a futile action because the pollen is much too sticky.

NON-POLLINATING HALICTID VISITORS OF  
*C. GUTTATUM*

Three species displayed various degrees of association with the orchid without acting as pollinators, as summarized in Table 5. *L. excisum* and *L. flavohirtum* landed on the flower but either did not enter the pouch or, if they did, were not able to climb the tunnel beyond the lower edge of the stigma. With a thorax height of 2–2.3 mm they are slightly too large to pass the bottlenecks at the stigma and anthers. *L. zonulum euronotum*, with a thorax height of 2.5–3.1 mm, is the largest of the halictids; it is much too large for *C. guttatum* although, interestingly, it is a pollinator of *C. yunnanense* (unpubl. data, this study). *Halictus yunnanicus* was only caught once on the wing and would be too large to pollinate the orchid.

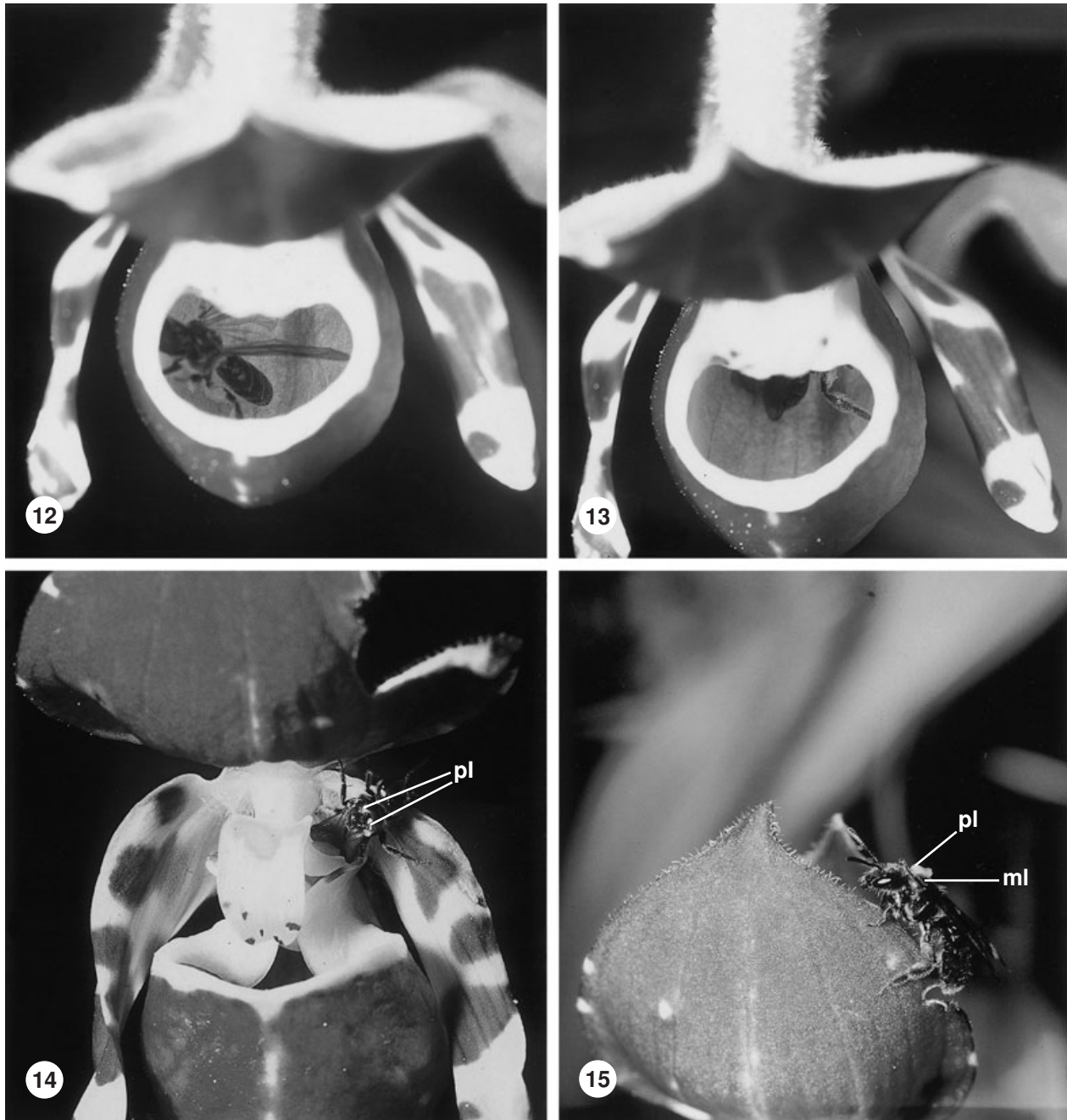
Small specimens of *Sphecodes* sp. nr. *hyalinatus* may be capable of exiting by the gap but would be, if at all, exceptional pollinators. As a parasite laying its eggs in the brood of other bees instead of provisioning its own young, the species is not dependent on frequent flower visiting like nonparasitic bees.

*C. GUTTATUM* POLLINATORS ON OTHER  
*CYPRIPEDIUM* SPECIES

With a thorax height of 1.1–1.8 mm, the pollinators of *C. guttatum* are too small to acquire pollen from the

**Table 5.** Behaviour of non-pollinating halictid visitors of *Cypridium guttatum*

<i>L. excisum</i>	One settled on sepal. One seen in pouch (not seen how entered), attempted unsuccessfully to climb the tunnel which was too narrow for this species, after 8 min finally left by entrance. Two advanced below sepal but did not fall into pouch and, after a few seconds, flew off to an <i>Anemone obtusiloba</i> where both were collected a few seconds later. Four advanced below sepal but subsequent behaviour could not be observed, except that none was able to climb the tunnel.
<i>L. zonulum euronotum</i>	One settled for a few seconds on sepal and flew off. One flew to grassy ground near flowers but flew off, returned exhibiting same behaviour 5 min later. One flew over <i>C. guttatum</i> assemblage without being attracted to them.
<i>L. flavohirtum</i> or <i>L. zonulum euronotum</i>	One settled briefly on sepal.
<i>L. excisum</i> or <i>L. flavohirtum</i>	One settled on rim of pouch, but its entrance was evidently too narrow to enter, flew off. One advanced below sepal but flew off after 5 s. One settled on sepal to groom itself, after 1 min flew off to settle on another flower's upper sepal, then flew off again. One settled on upper sepal of three different <i>C. guttatum</i> , once advancing below sepal but flew off after a few seconds.
<i>Lasioglossum</i> , probably <i>zonulum euronotum</i>	One flew over the flower assemblage without showing attraction.



**Figures 12–15.** Pollinators of *Cypripedium guttatum*. Fig. 12. *Lasioglossum clypeinitens*, having just tumbled into the pouch of *C. guttatum*, is attempting to escape by the entrance. Fig. 13. Failing to escape by the entrance, it climbs the back wall. Fig. 14. *L. sauterum* leaving the exit, having acquired a small pollen smear (pl). Fig. 15. *L. clypeinitens* climbed the sepal, having acquired a pollen smear; the bee is trying to wipe off the pollen with its middle leg (ml) – in vain, as the pollen is too sticky.

much larger *C. flavum* and *C. yunnanense*, which have exit gaps of 3.0–3.5 mm. Indeed, after entering these flowers they left rapidly and unhindered through the exit. Observations included two

*L. mystaphium* and four *L. virideglaucum* on *C. yunnanense*; one *L. clypeinitens* on *C. flavum* and four on *C. yunnanense*; and one *C. allodalum* each on *C. flavum* and *C. yunnanense*.

BEES OF OTHER FAMILIES AS POTENTIAL  
POLLINATORS OF *C. GUTTATUM*

Investigation of flowers of the surrounding vegetation yielded Andrenidae (eight species), Apidae (three species), Colletidae (two species) and Megachilidae (two species). None were seen to be attracted to, or carrying pollen of, *C. guttatum*. Yet two *Andrena* spp., another two new taxa discovered during our study, were pollinators of *C. flavum* (unpubl. data, this study).

HOVERFLIES AS POTENTIAL POLLINATORS OF  
*C. GUTTATUM*

Syrphidae were carefully watched, both on *C. guttatum* and other flowers, because some species are confirmed pollinators of *Paphiopedilum*. At least ten species of Syrphinae and nine of Milesiinae were collected. Of these, only *Melanostoma orientale* (Wiedemann), *Melanostoma* sp., and *Sphaerophoria* sp. nr. *nigritarsis* Brunetti were found to be small enough to be potential pollinators of *C. guttatum*. Only three specimens of the latter two syrphid species were seen to fly through the orchid cluster, without settling on any flowers. In addition, they would be too weak to extrude themselves through the exit of *C. guttatum*.

DISCUSSION

With observations of 11 successful and two unsuccessful pollen acquisitions (the latter due to depleted anthers) and details on how pollinators are trapped by *C. guttatum*, pollination of this slipper orchid is now better documented than all of the other species of *Cypripedium* with the exception of *C. calceolus*, for which over 80 pollen acquisitions were reported by Nilsson (1979).

Little or nothing is known about pollinator behaviour in the seven other *Cypripedium* species. There have been only seven direct observations of pollen acquisition or deposition in *C. parviflorum* (Guignard, 1886; Stoutamire, 1967), four in *C. acaule* (Stoutamire, 1967; Davis, 1986) and just one to three in *C. arietinum* (Stoutamire, 1967), *C. californicum* (Kipping, 1971), *C. candidum* (Catling & Knerer, 1980), *C. macranthos* (Sugiura *et al.*, 2001) and *C. reginae* (Guignard, 1886). In the latter, two additional pollen acquisitions by a syrphid fly and one by a beetle were observed (Vogt, 1990). However, these findings are based on mere eight hours observations and need further elucidation: the insects are likely to be accidental, illegal pollinators as *Cypripedium* are typically melittophilous.

Some indirect evidence also supports our findings. First, *Lasioglossum* (either *clypeinitens* or *virideglaucum*) carrying a smear of *C. guttatum* was observed hovering near the orchid. Secondly, except for the pol-

linator species, no other bee carried a smear of the orchid. The third is the finely tuned adaptations of *C. guttatum* to the morphology and behaviour of its pollinators while excluding potential pollinators lacking such requirements. Potential pollinators are either too large (*L. excisum*, *L. flavohirtum*, *L. zonulum euronotum*), or both do not voluntarily enter the narrow passages of the flowers and are too weak (Syrphidae), or showed no attraction to *C. guttatum* (Andrenidae, Apidae, Megachilidae, Colletidae, most of which are also too large). Since *C. guttatum* is also present in North America while *C. calceolus* is not (Atwood, 1985b and Cox, 1995, cited in Cribb, 1997: 149–150; and Cribb, 1997), *C. guttatum* is America's best studied slipper orchid pollination-wise.

At least three species of Halictidae were found to be pollinators of *C. guttatum*, viz. *L. virideglaucum*, *L. clypeinitens* and *L. sauterum*, while *L. mystaphium* is an almost certain pollinator and *L. allodalum* a probable one. *L. virideglaucum* and *L. clypeinitens* (23 and 11 specimens recorded, respectively, Table 1) were more frequently recorded probably due to their being more common in the area than *L. sauterum*, *L. mystaphium* and *L. allodalum* (1–3 specimens only), rather than because they are more regular pollinators. In fact, smaller species such as *L. mystaphium* are better suited to pollination because they need less effort to squeeze through the narrow passages than larger ones like *L. clypeinitens*. Furthermore, whereas *L. virideglaucum* is relatively widespread (Yunnan, Sichuan and Shansi provinces of China, and Japan), *L. sauterum* is not found in Japan, and *L. clypeinitens* and *L. mystaphium* have been reported only from Yunnan and one additional province each (Sichuan and Shansi, respectively) (Ebmer & Sakagami, 1985; Fan & Ebmer, 1992; Ebmer, Maeta & Sakagami, 1994; Ebmer, 2002). Thus, over wide areas of the vast range of *C. guttatum* there are no records of the pollinator species we observed and therefore it is virtually certain that vicariating halictid species assume the role of pollinators there.

Interestingly, all but one of the ten halictid species displayed a certain degree of attraction to *C. guttatum* (the exception, *H. yunnanicus*, was caught on the wing). In addition, *L. mystaphium*, *L. virideglaucum*, *L. allodalum*, and *L. clypeinitens* occasionally also visited two other slipper orchids, *C. yunnanense* and *C. flavum*. These bees are clearly not pollinators of these two orchids because they are much too small to acquire a smear. It is the largest halictid, *L. zonulum euronotum*, which is the pollinator of *C. yunnanense*. Hence the halictid's behaviour contrasts with that of the Andrenidae; none of which were associated with *C. guttatum*, or for that matter with *C. yunnanense*. Yet, significantly, two of the Andrenidae are pollinators of *C. flavum*. The halictids observed evidently



have a broader flower palette than the Andrenidae. The halictid's polylectic habits, which have also been noted by other authors (e.g. Westrich, 1989; A. Ebmer, pers. comm.), are also evident from their visitation of other flowers (Table 2): *L. virideglaucum* visited flowers of five genera of four families and *L. zonulum euronotum* eight genera of six families.

Halictidae also pollinate other slipper orchids: *C. arietinum* by *L. coeruleum* Robt., *C. parviflorum* by *L. pilosum* Smith, *L. coriaceum* Smith and *Agapostemon splendens* Lepeletier (Stoutamire, 1967); *C. calceolus* by *L. albipes* (F.), *L. morio* (F.), *L. calceatum* (Scop.), *L. quadrinotatum* (K.), *H. tumulorum* (L.) (Nilsson, 1979), *L. fulvicorne* (Kirby) and *L. laevigatum* (Kirby) (H. Bänziger, unpubl. data).

Since pollination is based on deception, the question arises whether *C. guttatum* mimics any reward-offering flower. Sugiura *et al.* (2002) proposed floral mimicry in *C. macranthos* var. *rebunense* (Kudo) Miyabe et Kudo of *Pedicularis schistostegia* Vved. (Orobanchiaceae). The sepal of *C. guttatum* is conspicuously white, as are the flowers of its neighbours *Anemone rivularis*, *Heracleum candicans* and *Crataegus oesbia*, or those of *Anemone obtusiloba* and *Rosa omeiensis* which are white with a yellow centre. While these flowers were sometimes visited by the halictids before or after *C. guttatum*, the bees also visited *Aster* sp. (pale violet petals and yellow centre), *Ligularia dictyoneura*, *Taraxacum dasypodium*, *Potentilla fruticosa* and *Euphorbia stracheyi* (a conspicuous deep yellow), *Salvia brachyloma* (violet blue) and *Polygonum macrophyllum* (pinkish violet). The flora is therefore too diverse and the halictids too polylectic for the evolution of a mimetic relationship. *C. guttatum* evidently exploits innate susceptibilities of the halictids (e.g. to white and white-violet harlequin colours contrasting with the green background). Nilsson (1979) also found no evidence of floral mimicry in *C. calceolus*.

Nilsson (1979) found that two components in the odour of *C. calceolus* were the same as the pheromones of two glands of some *Andrena*-pollinators. The cephalic pheromone attracts females and probably aggregates males (Tengö & Bergström, 1977), while the pheromone of the abdominal Dufour gland is used in and around the nest of these bees (Bergström & Tengö, 1974). Thus Nilsson argued that *Andrena* species might be deceptively induced to land on *C. calceolus* because of these substances. Furthermore, he pointed out that these pheromones might be rubbed off onto the hairs and other structures of the orchid by the struggling pollinator. He proposed that this was the reason why flowers that were already occupied or which had just been visited tended to be more attractive than virgin ones. We made similar observations with *C. guttatum* where a

similar deception may be at work. Yet it may also be that the bees struggling in the pouch had severed the scent glands, thereby releasing increased amounts of attractive volatiles, as there is evidence of this occurring in the case of *Paphiopedilum villosum* (Bänziger, 1996).

The slippery methods with which *C. guttatum* captures its pollinators contrasts with those in its congeners *C. yunnanense* and *C. flavum*. In these the bees crawl down the wide infolded flaps of the pouch, which are not slippery, and then enter the interior much like they enter a tubular flower such as *Salvia brachyloma* (unpubl. observ., this study). The staminode plays no direct role in capture, though it may initially function as a false nectar guide in attracting the bees from a distance.

The pollination strategies of *C. guttatum* are reminiscent of those seen in *Paphiopedilum* spp., although in the latter case the pollinators are hoverflies. The staminode has a direct and pivotal role in triggering the pollinator's capture; its slippery surface and adjunct flight interfering devices dispatch pollinators into the pouch. The staminode operates in three different ways.

In the first type, found in *P. rothschildianum* and *P. callosum*, the pollinators manage to grip the staminode for a few seconds while laying an egg before losing their hold. In the second, observed in *P. villosum* and *P. charlesworthii*, food-seeking pollinators try to grip a very slippery wart protruding from the staminode, losing their hold instantly. In the third, found in *P. parishii* and *P. bellatulum*, they grip the staminode's flattish surface, also without intent of laying, and slide off shortly afterwards. In the first type the pollination syndrome is based on 'perfidious' brood-site deception (leading to the death of the pollinator's progeny); in the second and third types it is based on 'opportunistic' food deception, possibly with a faint brood-site deception also at work (but without deleterious effects) (Atwood, 1985a; Bänziger, 1994, 1996, 2002).

The main difference between *C. guttatum* and *Paphiopedilum* spp. is that in the latter the pollinators grip the staminode while air-borne and tumble backward, while in the former they grip from a settled position and tumble forward.

Due to their unusual morphology, it seems strange that *C. guttatum* and *C. yatabeanum* have not been grouped in a separate subgenus. This has been done with the subgenera *Brachypetalum* and/or *Parvisepalum* of the genus *Paphiopedilum*, where a certain analogy exists (Karasawa & Saito, 1982; Atwood, 1984; Cox *et al.*, 1997; Cribb, 1998). Re-evaluation of the molecular, karyological, electrophoretic (e.g. Case, 2002), morphological and functional aspects of *C. guttatum* may accord it a more distinct status than on a sectional



level (as *Bifolia*). The evolution and the relationships of the many taxa in the Cyripedioideae are very complex and far from settled, as Aoyama & Karasawa (2002) also demonstrated. *C. guttatum* may not be a 'link' between *Paphiopedilum* and *Cypripedium*, like *Paphiopedilum*'s subgenus *Parvisepalum* (Chen & Tsi, 1984; Cox *et al.*, 1997), yet it may foreshadow how transition, possible multiple, between melittophily and myiophily, or vice versa, may have evolved in such specialized flowers as the slipper orchids.

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