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# The missing link: bee pollination in wild lady slipper orchids *Paphiopedilum thaianum* and *P. niveum* (Orchidaceae) in Thailand

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Rare calcicolous *Paphiopedilum thaianum* and *P. niveum* were studied in S Thailand, 2007–2011. Their flowers are rewardless kettle-traps, the pouch-like lips keeping pollinators prisoner for many minutes. To leave, they have to climb a «tunnel», past the stigma to one of two anthers, where they squeeze themselves out of the narrow exit, thereby acquiring an amorphous smear of sticky pollen. Because the flowers were unusual, being fragrant and conspicuously white, they were compared with two typically malodorous and mottled/yellow species, *P. godefroyae* and *P. concolor*. During more than 450 man-hours of watching, behaviour of all insects near, on and in the flowers was carefully observed to distinguish between legitimate and accidental pollinators, or mere visitors. Unexpectedly, melittophily was discovered in *P. thaianum* and *P. niveum*, the pollinators being the newly described halictid bee *Lasioglossum orchidodeceptum* and the meliponine bee *Tetragonula testaceitarsis*, respectively. Pollinators of *P. godefroyae* and *P. concolor* were, as expected, milesiine hoverflies, viz. *Eumerus nicobarensis* and *E. figurans*, respectively, confirming these two orchids as myiophilous like *Paphiopedilum bellatulum*. The five orchid species belong to the subgenus *Brachypetalum*, the second-most basal subgenus of *Paphiopedilum*. The most basal subgenus, *Parvisepalum*, is the closest relative of the mainly holarctic genus *Cypripedium*, in flower structure and in melittophily. Hence *P. thaianum* and *P. niveum* are proposed as the hitherto missing link between *Cypripedium* (via *Parvisepalum*) and the more derived *Paphiopedilum*, all myiophilous. The very similar *P. thaianum* and *P. niveum* were found to be reproductively isolated by enticing pollinators differing at family rank and by allowing pollen acquisition only by appropriately-sized bees, smaller in *P. thaianum*. This supports them as good species.

Oviposition on *Paphiopedilum dianthum* by syrphine hoverflies, supposedly visually misled by dark dots mistaken for aphids, the prey of the flies' progeny, is reassessed because oviposition is known to be olfactorily induced. The purported mixed bumblebee-blowfly pollination of *Cypripedium flavum* is also reassessed.

Keywords: Allomones, Aphididae, brood-site deception, *Eumerus*, food-deception, Halictidae, hoverflies, Meliponini, Milesiinae, oviposition, *Paphiopedilum concolor*, *P. godefroyae*.

## INTRODUCTION

Described in 2006 from South Thailand, *Paphiopedilum thaianum* Iamwiriyakul is among the most recent in a series of slipper orchid novelties. Actually, the orchid had long been known to local enthusiasts but they considered it as a dwarf form of *P. niveum* (Reichb. f.) Stein. Due to this, its recognition as a good species is, in fact, still much debated, even after an additional, biologically crucial, character was found in *P. thaianum*: its distinctly fragrant scent. Surprisingly, this remarkable character was omitted in the original description. Other species of the subgenus *Brachypetalum* and the rest of approximately 70 (Cribb 1998) less closely related

species of *Paphiopedilum* are, where noted, arguably faintly malodorous or more or less scentless to the human nose. The only exceptions are four of the eight species of the subgenus *Parvisepalum* which are distinctly fragrant, viz. *Paphiopedilum delenatii* Guillaumin, *P. malipoense* S. C. Chen & Z. H. Tsi, *P. jackii* H. S. Hua, and *P. hangianum* Perner & Gruss. *Paphiopedilum emersonii* Koop. & P. J. Cribb is only weakly fragrant (not perceived by all workers), whereas *P. armeniacum* S. C. Chen & F. Y. Liu, *P. micranthum* Tang & Wang and *P. vietnamense* Gruss & Perner apparently are not odorous to humans (Averyanov, pers. comm.; Kaiser, pers. comm.; Grell, pers. comm.). *Parvisepalum* is characterized by having flowers very similar to the genus *Cypripedium*; in *Brachypetalum* they are more *Paphiopedilum*-like except for the pouch margin being infolded all-round and for the very broad petals (Cribb 1998).

So far, pollination has been studied in some 9 species of *Paphiopedilum* (e.g. *P. callosum* (Reichb. f.) Stein, *P. charlesworthii* (Rolfe) Pfitzer, *P. dianthum* T. Tang & F. T. Wang, *P. parishii* (Reichb. f.) Stein, *P. rothschildianum* (Reichb. f.) Stein, *P. villosum* (Lindl.) Stein (Atwood 1985; Bänziger 1994, 1996, 2002; Shi *et al.* 2006, 2008). In all cases myiophily was found (one exception, see discussion) by hoverflies (Diptera, Syrphidae), deceived either by brood-site deception (e.g. in *P. callosum* and *P. rothschildianum*) or food-deception (most of the others). In the other genus of lady slipper orchids, the mainly holarctic *Cypripedium*, pollination has been studied in over a dozen species (e.g. *C. calceolus* L., *C. fargesii* Franch., *C. flavum* P. F. Hunt & Summerh., *C. guttatum* Sw., *C. japonicum* Thunb., *C. macranthos* Sw., *C. parviflorum* Salisb., *C. smithii* Schltr., *C. tibeticum* King ex Rolfe) where bees are pollinators (Hymenoptera: Andrenidae, Apidae, Halictidae, Megachilidae; exception see discussion) (mainly Müller 1868; Stoutamire 1967; Daumann 1969; Nilsson 1979; Sugiura *et al.* 2002; Bänziger *et al.* 2005, 2008; Li *et al.* 2006, 2009; Sun *et al.* 2009; Ren *et al.* 2011; Zheng *et al.* 2011). *Cypripedium* species are more or less fragrant and entice by food deception. So far, no sexual deceit, such as present in *Ophrys* spp. (e.g. Kullenberg 1961; Schiestl 2005; Schiestl *et al.* 2000) has been found in slipper orchids.

The aim of our study was threefold. First, to understand the reproductive strategy of *P. thaianum* and *P. niveum* in the hope that conservation of these rapidly vanishing rarities can be improved. Knowledge of pollinators is also important in cases where re-introductions to the original home become necessary (Grell *et al.* 1988).

Second, to investigate evidence for the orchids' adaptations to pollinators as an aid for solving the controversy around the rank of *P. thaianum*: does it entice different pollinators from those of *P. niveum*, with consequent distinct reproductive biology, thus underpinning the recognition of *P. thaianum* as a good species?

Third and most significantly, the discovery that *P. thaianum* and *P. niveum* are melittophilous whereas *P. bellatulum* (Reichb. f.) Stein had been shown to be myiophilous (Bänziger 2002), has important implications for the understanding of the evolution of slipper orchids in *Paphiopedilum* as well as in *Cypripedium*. Thus, for a more thorough understanding of the pollination syndrome in the whole subgenus *Brachypetalum*, the remaining species of *Brachypetalum*, *P. concolor* (Bateman) Pfitzer and *P. godefroyae* (God.-Leb.) Stein, were additionally investigated.

Pollination studies of slipper orchids are rather challenging because they tend to grow in sites of difficult access, are rare and, most frustratingly, infrequently visited

by pollinators. Hence pollen acquisition is sporadically seen and its deposition only rarely observed.

## MATERIALS AND METHODS

### *Study sites and habitat*

All species of the subgenus *Brachypetalum* we studied grew on limestone rocks. Mountaineering equipment was required to reach some of the sites (methods adapted from tree climbing as described in Bänziger (1996)). At other sites, one had to remain tied to ropes for safety during the day-long watching of the flowers at or near the edge of ravines.

*Paphiopedilum thaianum* was investigated at three sites: nearby hills at 390, 400 and 410 m a.s.l., near Phangnga, Phangnga Province, S Thailand. Porters were required for carrying rock climbing and bivouacking equipment for up to four days, along a steep, three hours ascent from the nearest hut. Primary tropical evergreen rain forest predominated on craggy limestone, a mixture of both labyrinth karst and tower karst (Whitmore 1975). The orchids rooted in limestone fissures or occasionally in mossy, leaf-litter pockets. Some were on ledges (Fig. 1) close or at the edge of vertical rock walls. Each of the three populations had a mere 5–12 flowering plants. They were scattered, so each of the 2–5 observers, working within calling distance, was able to watch only 1–2 flowers at one time. Flower watching sessions were 29–30 April, 2007, 24–25 March and 23–25 April, 2008, 5–8 April and 3–6 May 2009, and 25–26 February, 2010, for a total of 170 man-hours. Watching generally started 8–9 am and ended 4–5 pm, but on 29 April, 2007, one flower was watched throughout the night.

*Paphiopedilum niveum* was studied at five sites in S Thailand: hill near Ban Nai Chong, Krabi Prov., 100 m a.s.l., 13 May, 2010; hill NW of Kantang, Trang Prov., 230 m a.s.l., 14–15 May, 2 and 19–20 June; another hill nearby, 340 m a.s.l., 24–27 June, 2010; and two hills N of Satun, Satun Prov., 150 m a.s.l., 10–11 and 15–16 July, 2011. The habitat was similar to that of *P. thaianum*. However, *P. niveum* tended to root less in limestone fissures but mostly in humus pockets of limestone rocks (Fig. 4), and the plants grew far less scattered, so that up to 13 flowers could be watched by one observer. Total flower watching time was 149 man-hours.

*Paphiopedilum concolor* was investigated on three hills 2–6 km distance from each other, at 890–940 m a.s.l., S of Umphang, Tak Prov., W Thailand, on 16 May, 2008, 30–31 May and 2 June, 2009, 28–30 May, 2010, and 2–5 May, 2011. Habitat was tropical deciduous forest typical for craggy limestone. The plants grew in assemblages of 3–7, rooted in limestone fissures (Fig. 10) or in humus pockets. Flower watching time was 83 man-hours.

*Paphiopedilum godefroyae* was studied at three sites in S Thailand: two hills near Phangnga, a few km to the south of where *P. thaianum* was investigated, at 240 and 210 m a.s.l., 27 April 2008 and 10 April 2009; and a hill at Pha Phueng, Amphoe Phanom, Suratthani Prov., 170 m a.s.l., 8–10 May, 2009. Habitat was similar to that of *P. thaianum*. Populations grew in similar conditions to *P. niveum* (Fig. 16). Flower watching time was 49 man-hours. Since pollinators of *P. godefroyae* were unusually scarce, the orchid was additionally watched in a garden near

Tab. 1. Behaviour of pollinator *Lasioglossum orchidodeceptum* in flowers of *Paphiopedilum thaianum*. Numbers indicate specimens seen (or time spent in pouch), all females.

| Flying to flower | Landing on pouch | Crawling to pouch rim | Entrapment in pouch | Time spent in pouch (min) | Pollen acquisition |
|---|---|---|---|---|---|
| 21 (+ 9 no data) | 18 (+ 8 no data) | 12 (+ 10 no data) | 10 (+ 9 already in pouch, not seen how entrapped) | 0.5/0.5/0.5/2/ 2/3/3/3/4/4/5/ 5/5/15[1]/16[1] (+ no data in 4) | in 6, none in 3[3] (+ no data in 10[2,3]) |

[1] Extended time due to two bees present in pouch mutually hindering themselves in exiting.
[2] Fast leaving from exit prevented recording.
[3] Lack of pollen acquisition due to anthers' pollen being already depleted after several bees had been entrapped by the same flowers.

Chiang Mai, N Thailand, during 10 days April–June, 2010, for 33 hours by H.B. The garden was lush with plants but the habitat was very different from the orchid's original home. Although this allows a mere hint of possible pollinators involved, results nevertheless indicate potential vicariant pollinator species.

Observation methods, pollinator collecting, euthanizing etc. were as given in Bänziger *et al.* (2005). We emphasized study of the whole faunal spectrum in the vicinity of, on or in the orchids. This allowed a more reliable distinction between legitimate and accidental pollinators, or mere non-pollinating visitors. In slipper orchids successful pollination depends on the appropriate size correlation between the flower's exit gap and the pollinator's dimensions, primarily thorax height, but also to a minor extent the length of the pollinator – the longer the pollinator, the more difficult for it to bend while forcing itself out of the curved exit route (Tabs 10, 11). Small insects can escape by one of the two exits without acquiring pollen; too large ones will either perish by starvation at the bottom of the pouch unless they manage to escape by the entrance, or remain stuck in the «tunnel» opposite the stigma, or at one of the two anthers, often glued there by the sticky pollen. Care was taken not to touch the orchids to avoid contamination by sweat which, in our region, is attractive to hoverflies, halictids, *Isomyia* (Calliphoridae), and particularly to stingless bees (Apidae, Meliponini) (see below). However, avoidance was not always possible, especially when collecting entrapped insects, or when close smelling was required.

Photo credits: Figs 1–4, 6–8, 11–19 by H. Bänziger; Figs 5 and 9 by S. Pumikong; Fig. 10 by K. Srimuang.

Tab. 2. Behaviour of pollinator *Tetragonula testaceitarsis* in flowers of *Paphiopedilum niveum*. Numbers indicate specimens seen (or time spent in pouch), all workers.

| Flying to flower | Landing on pouch | Crawling to pouch rim | Entrapment in pouch | Time spent in pouch (min) | Pollen acquisition |
|---|---|---|---|---|---|
| 36 (+ 5 no data) | 24 (+ 3 no data) | 21 (+ 5 no data) | 21 (+2 already in pouch, not seen how entrapped) | 0.2/0.2/1/1/2/ 2/4/4/4/4/4/5/8 (+ no data in 10) | in 12[1], none in 5[2] (+ no data in 6[3]) |

[1] One additional *T. testaceitarsis* carrying pollen was collected while sucking sweat from the observer (H.B.). Microscopic examination confirmed *P. niveum* pollen.
[2] Possibly some of these are due to anthers' pollen depletion from previous entrapments.
[3] Fast leaving from exit prevented recording.

Tab. 3. Behaviour of pollinators *Eumerus figurans* and *E. nicobarensis* in flowers of *Paphiopedilum concolor*. Numbers indicate specimens seen (or time spent in pouch), all females except two *E. figurans* males.

| Flying to flower | Site of landing: pouch | or staminode | Entrapment in pouch | Time spent in pouch (min) | Pollen acquisition |
|---|---|---|---|---|---|
| *Eumerus figurans* | | | | | |
| 17[1] (+ 6 no data) | 2 | 6 (+ 4 not seen) (+ 11[1] data not clear) | 14[1] (+ 4 already in pouch, not seen how entrapped) | 0.5/0.5/0.5/0.5/ 0.5/1/1/1/1.5/ 1.5/2/4/5/18 (+ no data in 4) | in 4[1,2], none in 3[3,4] (+ no data in 9[5]; not applicable in 2[6]) |
| *Eumerus nicobarensis* | | | | | |
| 1 (+ 1 no data) | 0 | 1 (+ 1 data not clear) | 2 | 1/8 | 2 |

[1] One of which had a smear before entrapment, subsequently deposited on the stigma.
[2] An additional *E. figurans* with typical pollen clump from *P. concolor* was photographed on a leaf in the neighbourhood of the orchid (Fig. 14).
[3] Two of which males.
[4] Pollen at anthers already exhausted.
[5] Fast leaving from exit prevented recording.
[6] They exited the flower the wrong way (legs instead of thorax contacting anthers).

### *The breeding system of the slipper orchids*

No *in situ* experiments to assess our orchids' breeding system (apomixis, autogamy or xenogamy) were carried out because, due to their scarcity, all flowers had to be reserved for investigating natural pollination. However, data from nurseries show that there is no fructification in the absence of pollinators (thus excluding apomixis and autogamy), whereas manual pollination is known to yield high fructification rates, both when the flowers are outcrossed or selfed, proving that they are self-compatible. Thus our orchids' reproduction conforms to the vast majority of *Paphiopedilum* species.

### *Taxonomic notes on the pollinators and slipper orchids*

The pollinator of *P. thaianum*, at the time of our field research a new species of sweat bee (Hymenoptera, Halictidae), was described and appropriately named as *Lasioglossum orchidodeceptum* (Pauly & Bänziger 2011). The pollinator of *P. niveum* belongs to a taxonomically difficult group of stingless bees (Hymenoptera, Apidae, Meliponini). In Sakagami (1978) the pollinator keyed out as *Tetragonula laeviceps* Smith but Rasmussen & Michener (2010) showed that *T. laeviceps* sensu Sakagami was based on the wrong type species. According to Michener (pers. comm.) the appropriate name for the taxon from S Thailand is *T. testaceitarsis* (Cameron). The pollinators of *P. concolor* and *P. godefroyae* are hoverflies of the genus *Eumerus* (Diptera, Syrphidae, Milesiinae). Some species of *Eumerus* need taxonomic revision (Wyatt, pers. comm.), including the *splendens-aurifrons-niveipes-nicobarensis* complex, to which one the pollinators of *P. godefroyae* belongs, but *P. concolor*'s main pollinator, *E. figurans* Walker is not problematic. Bees, hoverflies and calliphorids were identified by H.B. from his long-term collections at the Department of Entomology and Plant Pathology, Faculty of Agriculture,

Figs 1–3. *Paphiopedilum thaianum*. — 1, flowering plant (arrow) in typical habitat; — 2, detail of flower; note large blotches inside pouch which distinguish it from *P. niveum*; e=exit, ep=entrance of pouch, pu=pouch, pt=petals, s=staminode, se=sepal, bar=10 mm; — 3, female halictid bee *Lasioglossum orchidodeceptum* squeezing itself out of the narrow exit, thereby acquiring a pollen smear; bar=2 mm. Figs 1–16 show natural events in original habitat.

Figs 4–5. *Paphiopedilum niveum*. — 4, three flowering plants (arrows) in typical habitat; — 5, detail of flower; bar=10 mm. — Figs 6–9. Worker meliponine bee *Tetragonula testaceitarsis* entrapped in *P. niveum*. — 6, at pouch bottom; — 7, climbing up «tunnel»; — 8, squeezing itself out of the exit while acquiring a pollen smear; — 9, leaving with a small yellow smear on thorax; a=anther, p=pollen, bar=2 mm.

Chiang Mai University (DEFACU) where vouchers of the present study are also deposited.

The classification of slipper orchids follows Cribb (1998).

## RESULTS

### *Functional morphology of the flowers*

The flowers of *P. thaianum* (Figs 2, 3) were 2.6–5.0 cm wide, 1.5–4.0 cm long, the pouch (lip) 1.1–1.9 cm wide, 1.5–3.6 cm long, its entrance 0.5 – 0.6 cm across, the exit gap 1.5–2 mm wide. They were conspicuosly white, inside the petals basally mostly with blue- to red-violet, rather fine dots, more scattered distally, the upper sepal dotted only basally, the pouch with quite large dots centrally from base to bottom, the flaps dotted or not, the staminode with a large, mostly greenish, sometimes yellowish, irregular but somewhat butterfly-shaped area. Outside the pouch was only occasionally finely dotted, but due to its thin wall, the inside blotches could show through.

The flowers of *P. niveum* (Figs 5, 8) were very similar to *P. thaianum* except for the larger size, 3.5–6.2 cm wide, 3.1–6.0 cm long, the pouch 1.4–2.3 cm wide, 2.0–3.6 cm long, its entrance 0.75–0.85 cm across, the exit gap 2–2.5 mm wide, the shape of the pouch less elongate, the dots inside the pouch only small and restricted between base and stigma, and the mark on the staminode tending to be more yellowish.

The flowers of *P. concolor* (Fig. 11) were 5.3–6.0 cm wide, 5.5–6.5 cm long, the pouch 1.2–1.7 cm wide, 2.5–3.5 cm long, the exit gap 2.3–2.7 mm wide. The colour was deep yellow with more or less evident, fine reddish dots, those along the center of sepal and petals often arranged in a longitudinal streak directed toward the center of the flower, the flaps and staminode often also dotted, though generally not on the two gibbosities of the staminode. Outside the pouch was only finely dotted.

The flowers of *P. godefroyae* (Fig. 19) were 3.7–8.3 cm wide, 3.4–6.2 cm long, the pouch 1.2–2.0 cm wide, 2.3–3.7 cm long, its entrance 0.9–1.1 cm across, exit gap 2.5–3.0 mm wide. The colour was white to pale creamy or pale greenish, mostly very strongly mottled on sepal and petals, the brown-violet dots often large and sometimes coalescing in longitudinal streaks directed to flower base, the flaps and staminode often also strongly mottled, the latter with a small, greenish to yellowish central blotch. Outside the pouch was rarely dotted, and then only basally and finely. The flower is very similar to *P. bellatulum*, though this is generally clearly mottled externally on pouch.

Tab. 4. Behaviour of pollinator *Eumerus nicobarensis* in flowers of *Paphiopedilum godefroyae*. Numbers indicate specimens seen (or time spent in pouch), all females.

| Flying to flower | Site of landing: pouch | or staminode | Entrapment in pouch | Time spent in pouch (min) | Pollen acquisition |
|---|---|---|---|---|---|
| 6 | 2 | 3[1] | 3 | 0.5/0.5/1 | in 1; (+ no data in 2[2]) |

[1] One attempted landing on staminode four times.
[2] Fast leaving from exit prevented recording.

Tab. 5. Supplementary data on pollinators observed in garden habitat, *Eumerus splendens*, *Graptomyza brevirostris* and *Syritta orientalis* in flowers of *Paphiopedilum godefroyae*. Numbers indicate specimens seen (or time spent in pouch), all females.

| Flying to flower | Site of landing: pouch | or staminode | Entrapment in pouch | Time spent in pouch (min) | Pollen acquisition |
|---|---|---|---|---|---|
| *Eumerus splendens* | | | | | |
| 3 | 1 | 2 | 2 | 1/3 | 2 |
| *Graptomyza brevirostris* | | | | | |
| 4 (+ 3 data not clear) | 2 (+ 2 data not clear) | 3 | 2 (+ 2 found drowned[1]) | 4/8 (+ 2 not applicable[1]) | 2 (+ 2 not applicable[1]) |
| *Syritta orientalis* | | | | | |
| 7 (+ 4 data not clear) | 2 (+ 5 data not clear) | 4 | 2 (+ 1 data not clear; + 3 found drowned[1]) | 0.3/1.5/30[2] (+ 3 not applicable[1]) | 1 (+ 1 not clear, + 3 not applicable[1]; + 1 stuck at exit[2]) |

[1] Drowning due to water-logged pouch caused by excessive watering.
[2] Too weak to exit, was manually eased out after 30 min.

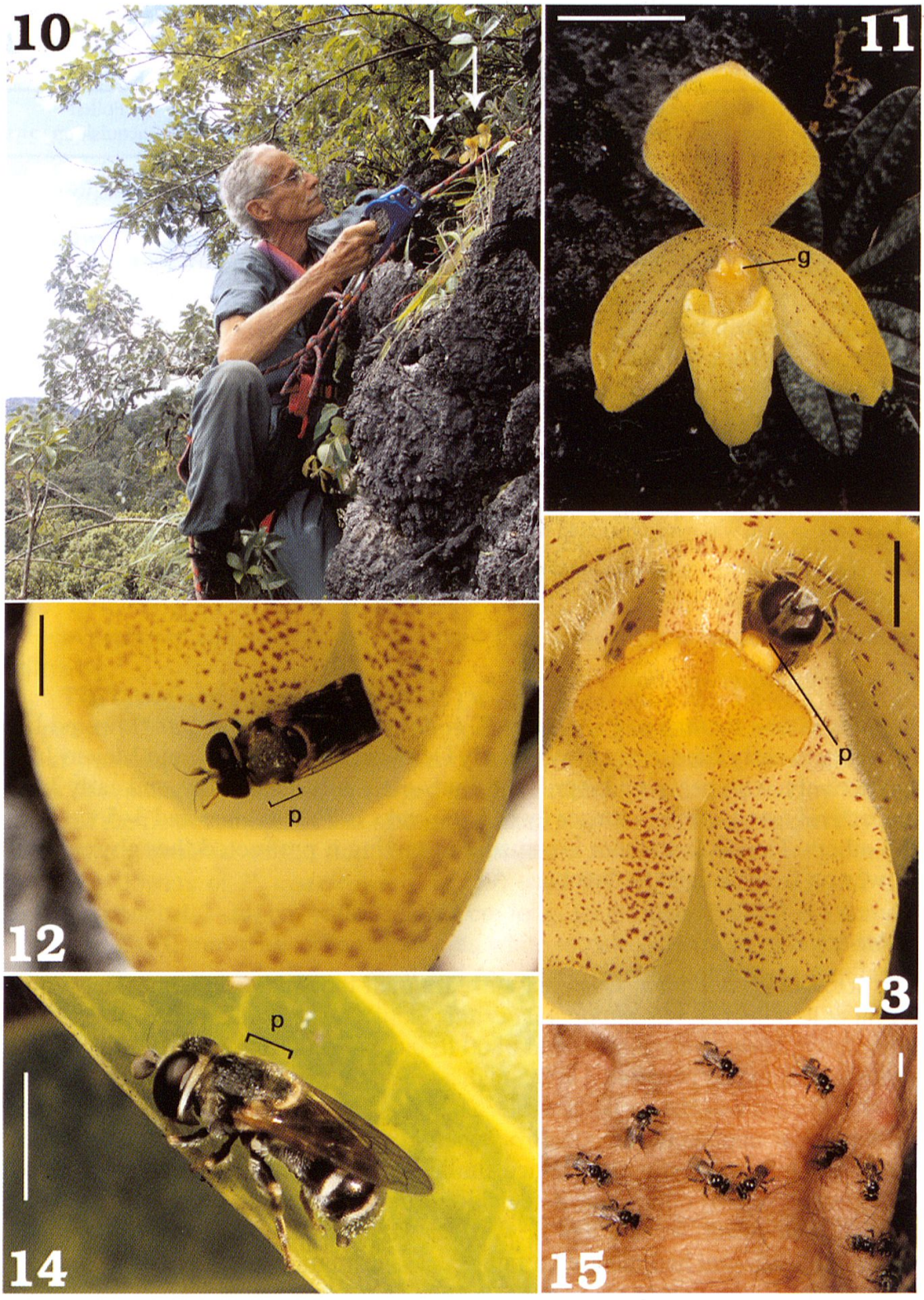
N.B. These pollinators are not considered legitimate until found to be so in the wild, although *Eumerus splendens* is a legitimate pollinator of wild *Paphiopedilum bellatulum*.

### *Flowering season and flower longevity*

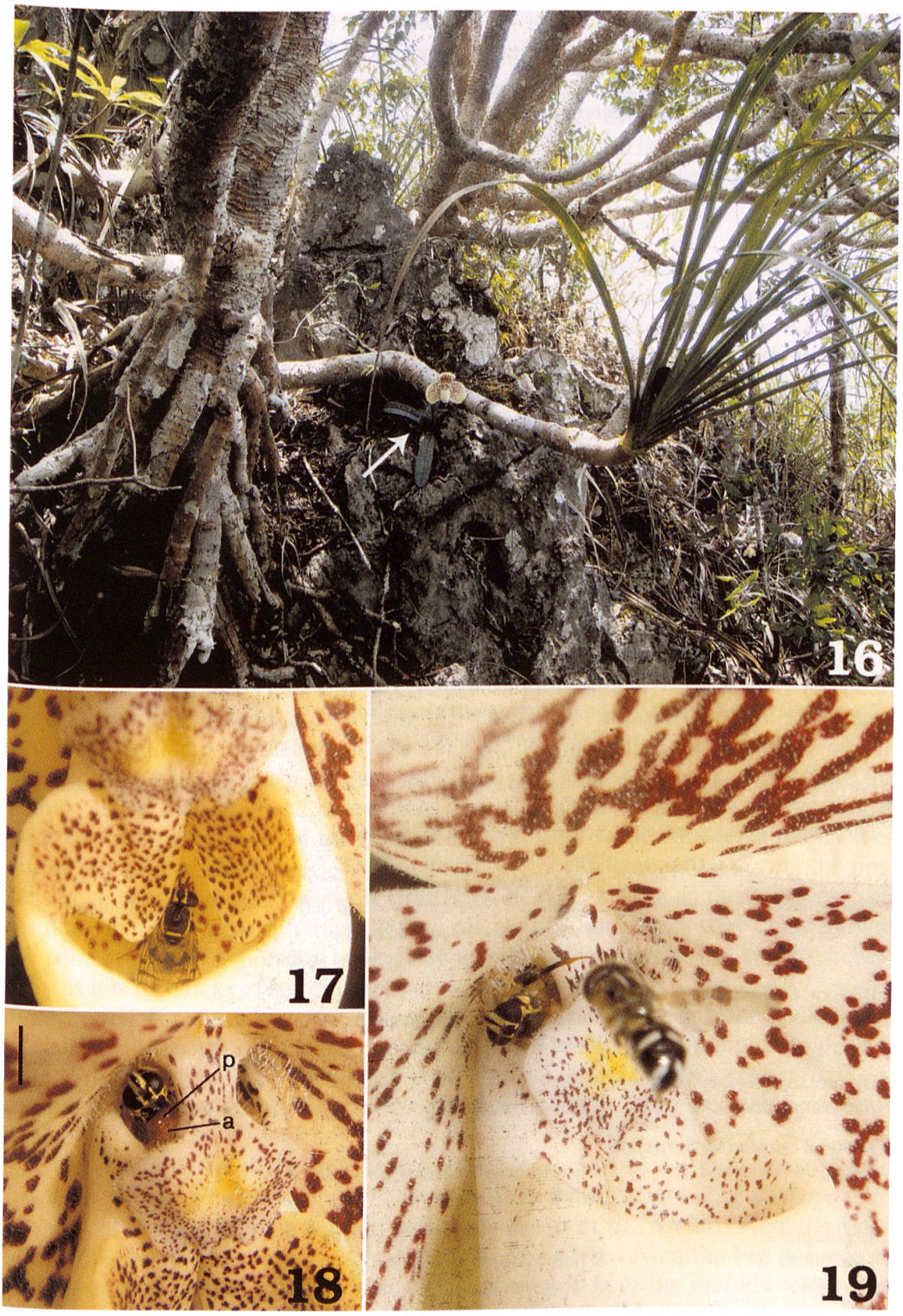
*Paphiopedilum thaianum*, *P. niveum*, *P. godefroyae* and *P. concolor* flowered late February to early June, early May to early October, March to July, and May to July, respectively, with peaks mid April, end June–early July, early May, and early June, respectively, and a flower longevity of 3–6 weeks in *P. thaianum* and 3–5 weeks in the others. Hence *P. niveum* is unusual in having a protracted though scattered flowering from August to October.

### *Scent release*

The scent of *P. thaianum* was pleasantly fragrant though weak, somewhat reminiscent of lemon grass (*Cymbopogon citratus* Stapf). It was barely perceptible shortly after dawn, became distinct around 0800 h, increased until around 1330 h when it was possible to just perceive it at 0.5 m distance downwind, slowly decreasing until 1800 h when it was barely perceptible. The odour of *P. godefroyae* was the strongest and most unpleasant among *Brachypetalum*, somewhat reminiscent of rancid butter and human perspiration, hence similar to *P. bellatulum* (Bänziger 2002) but more intensive. No odour was detectable to the human nose in *P. niveum* and *P. concolor*. However, when a live flower was wrapped in a plastic bag for a couple of hours, *P. niveum* had released a faint, pleasant fragrance which was clearly different from *P. thaianum*, whereas *P. concolor*'s odour was unpleasant and similar to *P. godefroyae*, though very weak. Populations of *P. concolor* from Khao Yai and Prachinburi (southern NE Thailand) are known to be weakly smelly.




Figs 10–11. *Paphiopedilum concolor*. — 10, three flowering plants (arrows) at the edge of a rock face being watched by H.B.; — 11, detail of flower; note the two gibbosities (g); bar=20 mm. — Figs 12–14. Milesiine hoverfly *Eumerus figurans*. — 12, entrapped female with a pollen smear (p) on the back, at pouch bottom; bar=3 mm; — 13, after depositing pollen on the stigma, it acquires a new smear (p) as it exits; — 14, female with a pollen smear (p) of *P. concolor* on a leaf. — Fig. 15. Meliponine bees (*Tetragonula* sp.) sucking sweat from the wrist of H.B. Bar=3 mm.




Figs 16–19. *Paphiopedilum godefroyae*. — 16, flowering plant in typical habitat (arrow); — 17, female milesiine *Graptomyza brevirostris* climbing up «tunnel»; — 18, sneaking out of exit while acquiring pollen (p), bar=3 mm; — 19, similar case with *Eumerus* sp. approaching staminode. Figs 17–19 are natural events in garden habitat.

Table 6. Actual and potential vistors on or near *Paphiopedilum thaianum*.

| Species | Behaviour | Comments |
|---|---|---|
| **Hymenoptera, Apidae, Anthophorini** | | |
| *Amegilla* sp. | 2 flew to flower, not landed | Too large to acquire pollen |
| **Hymenoptera, Apidae, Apini** | | |
| *Apis cerana* | 1 flew to flower, 2 flew past flower, 2 sucked human sweat | Too large to acquire pollen |
| *Apis florea* | 2 landed on pouch, 1 climbed to staminode but too large to fall into pouch | Too large to acquire pollen |
| **Hymenoptera, Apidae, Ceratinini** | | |
| *Ceratina* (*Neoceratina*) sp. 1 | 1 flew to staminode but did not land | Too small to acquire pollen |
| **Hymenoptera, Apidae, Meliponini** | | |
| *Heterotrigona apicalis* | Flying in area, not attracted to flower | |
| *Lepidotrigona terminata* | Sucked sweat, not attracted to flower | |
| *Lisotrigona cacciae* | Several sucked human tears, not attracted to flower | Too small to acquire pollen |
| *Lisotrigona furva* | Several sucked human tears, not attracted to flower | Too small to acquire pollen |
| *Pariotrigona klossi* | Many sucked human tears, not attracted to flower | Too small to acquire pollen |
| *Tetragonula laeviceps* | Sucked from sweat contaminated vegetation and human skin, not attracted to flower | |
| *Tetragonula fuscobalteata* | Sucked from sweat contaminated vegetation and human skin, not attracted to flower | |
| *Tetragonula sirindhornae* | 1 entrapped in pouch, unable to exit; further specimens sucked sweat | Slightly too large to acquire pollen |
| *Tetragonula testaceitarsis* | Sucked from sweat contaminated vegetation and human skin, not attracted to flower | |
| *Tetragonula* cf. *minangkabau* | 2 specimens were entrapped and left by exit, at least 1 acquired a little pollen; further specimens sucked sweat | Accidentally acquired pollen |
| **Diptera, Calliphoridae** | | |
| *Idiella mandarina* | Sucked human sweat, not attracted to flower | |
| **Diptera, Syrphidae, Milesiinae** | | |
| *Eumerus nicobarensis* | 1 found dead in pouch | Too large to acquire pollen |
| **Diptera, Syrphidae, Syrphinae** | | |
| *Episyrphus alternans* | 4 flew in neighbourhood, not attracted to flower | |
| **Lepidoptera** | | |
| Lycaenidae | 1 flew to flower, not landed | Too large to enter pouch |
| Hesperidae | 1 landed on pouch, proboscis fumbled in pouch | Too large to enter pouch |
| Pieridae | 1 flew to flower, not landed | Too large to enter pouch |

No Halictidae besides *Lasioglossum orchidodeceptum* were caught, but *Pachyhalictus burmanus* was present in nearby hills.

*Fructification*

Due to the remoteness of the study sites, so far only *P. thaianum* has been investigated for capsule formation. The 17, 21 and 8 flowers checked 2007–2009 produced 13, 14 and 5 capsules, respectively, a three year average of 70 %. This compares favourably with *P. bellatulum* where 41–92 % of the flowers developed a capsule, a six-year average of 66 %, based on 12–55 flowers per year (Bänziger 2002).

*Behaviour of pollinators*

The pollinators of *P. thaianum* and *P. niveum*, halictid bee *L. orchidodeceptum* and meliponine bee *T. testaceitarsis*, respectively, approached the orchids in similar fashion. The flowers' white contrasted starkly against the greenish or dark background, although white lichens on rocks were confusingly similar. When near the flower the bees often flew in a zig-zag manner (indicative of olfactory guidance), before flying quite straight to the flower, possibly guided/attracted by the greenish to yellowish blotch on the staminode. Generally they landed on the pouch, somewhat in front and below the entrance, then crawled toward the rim surrounding the entrance and, to some extent, along or over the infolded rim. Because the movements were rather fast, it was not clear whether they then lost grip and fell to the bottom of the pouch and then thrashed around, or crawled down a bit further to reach the bottom in control of their movements. Probably both occurred, since a furious thrashing was not always observed. At the bottom (Figs 6, 7), they might rest briefly but then crawled around and attempted to climb the frontal and lateral walls to escape by the entrance. This was rarely successful though an occasional wing-beating and flying succeeded in delivering them from the temporary prison. The lateral and front walls are too steep and overhang at the top, unlike the hind wall which, studded with hairs to grasp, channelled them (Fig. 7) past the stigma and on to the anthers. Here they acquired an amorphous smear of sticky pollen onto the thorax back (occasionally some on the head and wing base) while squeezing themselves out of the narrow exit (Figs 3, 8–9). The forces/mechanism acting during the process have been explained in detail (Bänziger 1996). As soon as the bees emerged from the exit they generally rapidly flew off, though sometimes they climbed onto the petal to rest for a moment, attempting to wipe off the pollen, but never successfully as it is too sticky. The sequences are summarized in Tabs 1 and 2. All *L. orchidodeceptum* were females, six acquired pollen, in 10 additional cases the pollen was exhausted after several bees had already swept the anthers. (Normally a single pollinator removes much of the pollen.) All *T. testaceitarsis* were workers, 12 acquired pollen, in 10 additional cases pollen may have been swept by previous workers.

The behaviour of the pollinators of *P. concolor* (mainly milesiine syrphid *Eumerus figurans* but less often *E. nicobarensis* Schiner) and *P. godefroyae* (*E. nicobarensis* and, in garden habitat, milesiines *Eumerus* sp., *Syritta orientalis* Macquart and *Graptomyza brevirostris* Wiedemann), differed from the bee pollinators of *P. thaianum* and *P. niveum* mainly in their approach to the orchids. The milesiines must have been attracted by the odours and possibly by the mottling. The convergent streaks on petals and sepal, and the gibbosities on the staminode, may have helped guide the insects toward the latter. At about 5–10 cm in front of the flowers they reduced flight speed and cautiously approached the staminode (Fig. 19).

Upon arrival, however, they instantly lost grip on it and tumbled into the pouch entrance. Occasionally they flew so low as to graze or hit the rim of the pouch, thereby falling into the entrance before reaching the staminode. Much thrashing occurred in the pouch. Subsequent phases were essentially the same as in bee pollinators (Figs 12, 13, 17–19). Observed sequences are summarized in Tabs 3–5. Two of the 18 *E. figurans* entrapped by *P. concolor* were males, the other milesiines were all females. In *P. concolor*, four *E. figurans* (Figs 12–14) and two *E. nicobarensis* acquired pollen, two *E. figurans* delivered it on stigmas (cf. Fig. 12). In *P. godefroyae*, one *E. nicobarensis* acquired pollen (besides several of the milesiines of the garden habitat (Tab. 5)).

*Illegitimate pollinators, non-pollinating visitors and co-occurring insects*

Below are treated insects which may have exhibited part of the following behavioural sequence: were in close proximity to the orchids, were attracted to or alighted on them, were entrapped (rare) or acquired pollen (once, unexpectedly). They are considered unlikely pollinators because they had: (i) an inappropriate size, (ii) a behaviour not conducive to pollination, (iii) no close taxonomic relationship to confirmed pollinators of that particular orchid species. At most they may have acquired pollen accidentally and were not actual pollinators. (It should be noted that it would be more exact to replace «illegitimate (accidental) pollinator» by «illegitimate (accidental) pollen acquirer». Actual pollination, i.e. pollen delivery, must be exceptionally rare in such insects, hence better mention that they simply acquired pollen.)

The most common visitors of flowers (all species) in close vicinity of our orchids were not their pollinators. Most prominent were meliponine bees, especially at *P. thaianum* and *P. concolor* sites, where they could outnumber pollinators by a factor of 10 to more than 100 overall. Also fairly common at *P. concolor* sites were *Isomyia* spp. (non-carrion breeding blowflies, Calliphoridae) and to some extent halictid bees and hoverflies. Besides the rich flora of the sites, a main source for attraction of these visitors was a feature typical for hot and humid habitats: human sweat. They sucked it from skin (Fig. 15), clothes and contaminated vegetation, but the minute *Pariotrigona* and *Lisotrigona* bees preferred sipping tears from human eyes (Bänziger *et al.* 2011). Some of these visitors, by mere chance or due to sweat contamination, also approached the orchids, settled on them, and a few fell into or «intentionally» entered the pouch. In the few cases where flower and insect size matched, they could illegitimately acquire pollen. Observed behaviours are summarized in Tabs 6–9, the visitors' sizes in Tab. 11.

However, another reason for the prevalence of meliponines was the presence of many nests in the orchids' neighbourhood, i.e. from a dozen to a few 100 meters distance, well within the foraging ranges of all but the smallest species. At the main *P. thaianum* site were 11 nests of five species within a 30 m radius, including that of tear drinking *Pariotrigona klossi* (Schwarz) (*loc. cit.*), at *P. concolor* sites were 9 nests of six species within a radius of 50 meters. But at the *P. niveum* sites no nest was found and meliponines were far less common. As eusocial bees their nests have a few hundred to tens of thousand workers (Michener 1974; Roubik 1989; Chinh *et al.* 2005), hence their prevalence. Other bees, non-Apini and many Halictidae (cf. Tabs 6–9), are non-eusocial (eusocial halictids have very small numbers of workers (Michener, pers. comm.), rarely more than ten), therefore were not so common.

Tab. 7. Actual and potential vistors on or near *Paphiopedilum niveum*.

| Species | Behaviour | Comments |
|---|---|---|
| **Hymenoptera, Apidae, Anthophorini** | | |
| *Amegilla* sp. | 1 flew in neighbourhood, 1 to flower, no landing | Too large to acquire pollen |
| **Hymenoptera, Apidae, Ceratinini** | | |
| *Ceratina* (*Neoceratina*) sp.1 | 4 settled on pouch or flew to staminode, 2 entered pouch, quickly out of exit | Too small to acquire pollen |
| *Ceratina* (*Ceratinidia*) sp. | Twice attempted entering by exit | Too large to acquire pollen |
| **Hymenoptera, Apidae, Meliponini** | | |
| *Lepidotrigona terminata* | Sucked sweat, not attracted to flower | |
| *Pariotrigona klossi* | Sucked human tears, not attracted to flower | |
| *Tetragonula laeviceps* | Sucked sweat from contaminated vegetation and human skin, not attracted to flower | |
| **Hymenoptera, Halictidae** | | |
| *Hoplonomia punctulata* | Sucked from sweat contaminated vegetation | Too large to acquire pollen |
| *Pachyhalictus burmanus* | Sucked sweat, not attracted to flower | |
| **Hymenoptera, wasps** | | |
| Large unidentified wasp | Landed on pouch, too large to fall into pouch | Too large to acquire pollen |
| **Diptera, Syrphidae, Milesiinae** | | |
| *Eumerus rufoscutellatus* | Flew 3 times to flowers, once settled across rim of pouch and staminode, did not enter flower | Too large to acquire pollen |
| Unidentified large syrphids | 5 attempted settling on staminode, only twice successful, but too large to fall into pouch | Too large to acquire pollen |
| **Diptera, Calliphoridae** | | |
| *Isomyia* sp. | 2 in pouch, 1 too large and weak to exit, 1 left by the entrance, 1 did not enter | Too large to acquire pollen |
| *Idiella mandarina*[1] | Settled twice on petal, did not enter pouch | Too large to acquire pollen |

[1] Identification uncertain because entrapment was very brief.

Lepidoptera (e.g. *Papilio aristolochiae* and diurnal sphingids), much larger than the flower, settled on or hovered over it, fumbling with their proboscis in the pouch. Pollen is too sticky to be removed by proboscis.

## DISCUSSION

The pollinators of *P. thaianum* and *P. niveum* are evidently bees, viz. halictid *L. orchidodeceptum* and meliponine *T. testaceitarsis*, respectively (Tabs 1, 2, Figs 3, 6–9). This is the first record of a stingless bee species pollinating a slipper orchid. We consider the acquisition of a little pollen from *P. thaianum* by one of two specimens of *Tetragonula* sp. cf. *minangkabau* (Sakagami & Inoue) as accidental. Meli-

ponines were the most common insects at the *P. thaianum* sites. If *T.* sp. cf. *minangkabau* were a legitimate pollinator, then it should have acquired pollen more often than *L. orchidodeceptum*. Of the other 8 meliponine species present, only one specimen of *T. sirindhornae* (Michener & Boongird) was entrapped – too large to leave by the exit. None of the remaining species was attracted to the orchid. Another visitor too big to leave by the exit was one hoverfly *E. nicobarensis*, found dead in the pouch. In *P. niveum* no illegitimate pollinator was found. Two non-pollinator species fell into the pouch, the xylocopine bee *Ceratina* sp. 1 and the fly *Isomyia* sp. (Tab. 7), both twice, but were too small or too large to acquire pollen, respectively. The finding of only female *L. orchidodeceptum* in *P. thaianum* may be due to the tendency of male halictids to appear much later in the season (Ebmer, pers. comm.; Pauly, pers. comm.). Workers only in *P. niveum* is normal since in Meliponini queens do not forage and males only exceptionally (e.g. Boongird & Michener 2010).

Pollinators of *P. concolor* and *P. godefroyae* were milesiine hoverflies, mainly *E. figurans* and *E. nicobarensis*, respectively (Tabs 3, 4, Figs 12–14), the latter also as an uncommon pollinator of *P. concolor*. The limited field data on *P. godefroyae* were corroborated by observations in a garden habitat: pollen acquisition was again by milesiines, viz. *Eumerus splendens*, *G. brevirostris* and *S. orientalis* (Tab. 5, Figs 17–19). Female pollinators only (except two male *E. figurans*) conforms to findings in other myiophilous *Paphiopedilum*, viz. males are uncommonly involved. Except when there is brood-site deception, the reason for this is not yet plain (possible explanations see Bänziger 1996; see also below). It is noteworthy that *P. concolor* sequestrated 8 additional visitor species of various families in its pouch (Tab. 8). However, none acquired pollen as they were either too small or too large. Only *L. albescens* (Smith) was of appropriate size, but it left by the entrance. This large and diverse number of entrapments reflects the insect richness at this orchid's sites (cf. Tab. 8). Entrapment of many non-pollinating insects has also been recorded in some other slipper orchids, e.g. *Cypripedium calceolus* (Nilsson 1979): Hymenoptera (more than 9 species, besides 6 andrenid and 5 halictid pollinators), Diptera (nearly 20 spp.), Coleoptera (7 spp.), Lepidoptera and Thysanoptera. Another factor probably contributing to the visiting or entrapment of non-pollinators in *P. concolor* was contamination with sweat, sought by many insects. This was less evident at the sites of *P. niveum* and *P. thaianum* because regular afternoon rains washed off the sweat from the vegetation, but conspicuous at the sites of *P. concolor* because of consecutive sunny days. A third factor was the presence of many meliponine nests, except at *P. niveum* sites where none was found.

It is likely that our orchids are not dependent on a single pollinator species and that closely related halictids, meliponines and milesiines may vicariate them in other areas – the pollinators of *P. godefroyae* in garden habitat (Tab. 5) are a good example.

The results for *P. godefroyae* agree with those for the very similar *P. bellatulum*, pollinated by milesiine *E. splendens* (Bänziger 2002). The results with *P. concolor* were expected because, despite generally being more yellow and often finer-mottled, its odour is similarly unpleasant as in *P. bellatulum* and *P. godefroyae*, even though in many populations *P. concolor*'s odour was not perceptible to humans. On the other hand, melittophily in *P. thaianum* and *P. niveum* was,

except for their scents, a surprise. All studied *Paphiopedilum* had hoverflies as pollinators (Atwood 1985; Bänziger 1994, 1996, 2002; Shi *et al.* 2006, 2008). Only *P. micranthum* is bee pollinated, by apids *Anthophora villosula* Smith and *Pyrobombus flavescens* (Smith) (Bänziger & Shi, in Bänziger *et al.* 2008, p. 61). As a member of the subgenus *Parvisepalum* Karasawa & Saito (1982), its flowers are rather similar to bee pollinated *Cypripedium* and quite different from *P. thaianum* and *P. niveum*. However, these species resemble *Parvisepalum* in their fragrant scent (very weak to humans in *P. niveum*, as it is in some *Parvisepalum*). This scent is presumably the reason, as in so many melittophilous flowers, for the attraction of bees. Hence, in relation to pollination, *P. thaianum* and *P. niveum* are the hitherto missing link between the similarly melittophilous *P. micranthum* (and presumably the other 7 species of *Parvisepalum*) and, through their closest relatives (myiophilous *P. bellatulum*, *P. concolor* and *P. godefroyae*), the remaining 60+ species of *Paphiopedilum*, all myiophilous so far as known.

In their description of lady slipper *P. malipoense* Chen & Tsi (1984), they noted that morphologically it was intermediate between *Paphiopedilum* and *Cypripedium* and proposed it to be a missing link between the two genera. This was contested by some authorities on the ground that it is based on superficial similarities due to pollination adaptations, whereas the most important characters are all advanced, hence far from being close to basal *Cypripedium*. However, molecular analyses (Cox *et al.* 1997) proved Chen & Tsi right: *Parvisepalum* and *Brachypetalum* are indeed the basal and second-most basal subgenera and hence the nearest links to *Cypripedium*. The anthophorine and bombine bee pollinators of *P. micranthum* further corroborate Chen & Tsi's hypothesis. What was still lacking was a direct link to myiophilous *Paphiopedilum* – our *P. thaïanum* and *P. niveum*.

*Parvisepalum*'s main distribution is in subtropical southern China and northern Vietnam, some 1500 km north of *P. thaianum* and *P. niveum*, which might weaken the view that they are a link between the two subgenera. However, one species, *P. delenatii* Guillaumin, occurs in tropical southern Vietnam (Averyanov *et al.* 1996). Further, only some 18 000 years ago at the peak of the last glaciation, the region had a strongly seasonal climate with a «savanna corridor» reaching Java and Sulawesi (Morley & Flenley 1987). *Parvisepalum* probably shifted its distribution down the Malay Peninsula and during the subsequent warming phase they might have gone extinct in the Peninsula.

Pollination of *P. bellatulum*, *P. concolor* and *P. godefroyae* by milesiine instead of syrphine hoverflies is significant. Recent trends, especially in secondary botanical literature on orchid pollination, increasingly take for granted the hypothesis that dark dots on orchids are attractive to hoverflies because mistaken for aphids. However, unlike syrphines (exceptions see Tab. 3, Bänziger 1996), milesiine pollinators are not aphidophagous in the larval stage, hence attraction, if any, works because the dots are perceived only as conspicuous *Saftmale* (nectar guides), as they are by bumblebees (Kugler 1970) and calliphorid flies (Steiner 1948). Also, it is well-known that the large majority of aphids are not dark but of various green and yellow shades, often contrasting little with their substrate, but such aphids are also laid at (hoverflies do not oviposit on but near aphids). Some species are not aphid-like, e.g. *Mollitrichosiphum*, *Greenidea*, *Greenideoida* have strongly elongate bodies and extremely long siphunculi (Raychaudhuri 1956; Ghosh *et al.* 1970;

Tab. 8. Actual and potential vistors on or near *Paphiopedilum concolor*.

| Species | Behaviour | Comments |
|---|---|---|
| **Hymenoptera, Apidae, Allodapini** | | |
| *Braunsapis hewitti* | Sucked from sweat contaminated vegetation and human skin; on *Litsea* flowers (Lauraceae) | |
| **Hymenoptera, Apidae, Anthophorini** | | |
| *Amegilla* sp. | Entered pouch, rapidly left by entrance | Too large to aquire pollen |
| **Hymenoptera, Apidae, Apini** | | |
| *Apis cerana* | Sucked sweat from humans, never seen flying to flower | |
| **Hymenoptera, Apidae, Ceratinini** | | |
| *Ceratina chiangmaiensis* | Sucked sweat from skin | Too small to acquire pollen |
| *Ceratina lieftincki* | Sucked sweat from skin | Too small to acquire pollen |
| *Pithitis* sp. | Sucked sweat from skin | |
| **Hymenoptera, Apidae, Meliponini** | | |
| *Heterotrigona apicalis* | Flying in area, not attracted to flower | |
| *Heterotrigona melanoleuca* | Flying in area, not attracted to flower | |
| *Lepidotrigona doipaensis* | Sucked from sweat contaminated vegetation and skin | |
| *Lepidotrigona flavibasis* | Sucked from sweat contaminated vegetation and skin | |
| *Lepidotrigona nitidiventris* | Flying in area, not attracted to flower | |
| *Lepidotrigona terminata* | Sucked from sweat contaminated vegetation and skin, not attracted to flower | |
| *Tetragonula laeviceps* | Twice on flower, once in and out of pouch, not seen how trapped and escaped | Too small to acquire pollen |
| *Tetragonula testaceitarsis* | 9 times on flower, 3 times fallen into pouch, only once out of exit, no pollen acquired | Slightly too small to acquire pollen |
| **Hymenoptera, Halictidae** | | |
| *Homalictus latitarsis* | 4 on flowers of *Litsea* sp. (Lauraceae) | Too small to acquire pollen |
| *Lasioglossum albescens* | 4 sucked from sweat contaminated vegetation and human skin, 2 sucked sweat from pouch and sepal, 1 fell from staminode but climbed out from entrance to continue sweat-sucking | Slightly too small to acquire pollen |
| *Lasioglossum perihirtulum* | 1 on *Litsea* flower, 1 on human skin | Too small to acquire pollen |
| *Lasioglossum* cf. *salwinicum* | Sucked sweat | Too small to acquire pollen |
| *Lasioglossum* sp. 1 | 2 on human skin | Too small to acquire pollen |
| *Lasioglossum* sp. 2 | 1 flew to sepal several times, flew into pouch and flew out of entrance | Too small to acquire pollen |
| *Lasioglossum* sp. 3 | 1 on human skin | Too small to acquire pollen |
| *Lasioglossum* sp. 4 | 1 zigzagging in front of flower, 1 settled briefly on sepal | Too small to acquire pollen |
| *Lasioglossum* sp. 5 | 1 on human skin | Too small to acquire pollen |
| *Lasioglossum* sp. 6 | 2 on human skin | Too small to acquire pollen |
| *Pachyhalictus burmanus* | Settled briefly on sepal, 1 sucked human sweat | Too small to acquire pollen |
| *Pachyhalictus reticulosus* | 2 on *Litsea* flowers | Too small to acquire pollen |

Tab. 8 (continued)

| | | |
|---|---|---|
| **Diptera, Calliphoridae** | | |
| *Hypopygiopsis infumata* | Sucked from sweat contaminated box | Too large to acquire pollen |
| *Idiella mandarina* | Sucked human sweat, not attracted to flower | |
| *Isomyia*, 5 species | Sucked from sweat contaminated vegetation and human skin | Too large to acquire pollen |
| *Stomorhina discolor* | Sucked human sweat, not attracted to flower | |
| **Diptera, Stratiomyidae** | | |
| *Clitellaria* sp. | 1 fell into pouch, came out by entrance, 1 settled briefly on pouch, flew off | Too large to acquire pollen |
| **Diptera, Syrphidae, Milesiinae** | | |
| *Eumerus aeneithorax* | Sucked sweat from skin | Too small to acquire pollen |
| *Eumerus aurifrons* | 4 sucked sweat | Too small to acquire pollen |
| *Eumerus rufoscutellatus* | 1 fell into pouch but climbed out of entrance, several sucked sweat on skin and vegetation | Too large to acquire pollen |
| *Graptomyza brevirostris* | Several sucked sweat from skin | Appropriate size but not seen entrapped |
| **Diptera, Syrphidae, Syrphinae** | | |
| *Allograpta robinsoni* | Sucked sweat from skin, not attracted to flower | |
| *Asarkina consequens* | Sucked from sweat contaminated vegetation, not attracted to flower | |
| *Dideopsis aegrota* | Sucked sweat from skin, not attracted to flower | |
| *Episyrphus alternans* | Sucked sweat from skin, not attracted to flower | |
| *Paragus* sp. nr. *politus* | Fell from staminode into pouch, quickly climbed out of exit | Too small to acquire pollen |

Ghosh *et al.* 1971), and still others are not readily recognizable as aphids, like *Pseudoregma* which can form immense ($10^5$ individuals), densely packed colonies enveloping bamboos in a grey-green sheet (Aoki *et al.* 2007). Yet they are also oviposited at by syrphines. While pointing out that it is the dark dots with hairs on the petals which are similar to aphids, rather than Atwood's (1985) suggested minute papillae on the staminode, Bänziger (1996, 2002) also stressed that such hairy dots could be osmophores. He proposed that these or other glands on *P. rothschildianum* and *P. callosum* probably release potent allomones imitating the odour released by aphids, thus misleading hoverflies to oviposit. He found no oviposition on *P. parishii* (*loc. cit.*) despite the presence of such dark blotches and concluded they had no such function. Indeed, its main pollinator *Allograpta robinsoni* (Curran) infrequently settled near, or followed the dark dots as guides, but most often landed at the papillose tip of the petal, probable site of osmophores. Intriguingly, this is also the spot most often alighted on by another syrphine, *Episyrphus balteatus* (De Geer), on the very similar *P. dianthum* where, remarkably, oviposition occurred in SW China (Shi *et al.* 2006, 2008). But oviposition near or at the dark blotches in this species was much less frequent and only once on the staminode, the site most densely oviposited in *P. rothschildianum* and *P. callosum* (Atwood 1985; Bänziger 2002) and the very spot from where the pollinators fell into the pouch, including in *P. dianthum* and *P. parishii*. Hence in *P. dianthum* entrapment was not the direct cause of oviposition. Attraction to flowers and aphids, and oviposition there, by hoverflies is elicited by a complex interaction of cues, object of much research (e.g.

Tab. 9. Actual and potential vistors on or near *Paphiopedilum godefroyae*.

| Species | Behaviour | Comments |
|---|---|---|
| **Hymenoptera, Apidae, Ceratinini** | | |
| *Ceratina* (*Neoceratina*) sp. 2 | 2 sucked from sweat contaminated vegetation and human skin, not attracted to flower | Too small to acquire pollen |
| **Hymenoptera, Apidae, Meliponini** | | |
| *Lisotrigona cacciae* | Many sucked human tears, not attracted to flower | Too small to acquire pollen |
| *Tetragonula fuscobalteata* | Sucked from sweat contaminated vegetation and human skin, not attracted to flower | Too small to acquire pollen |
| *Tetragonula laeviceps* | Sucked from sweat contaminated vegetation and human skin, not attracted to flower | Too small to acquire pollen |
| **Hymenoptera, Halictidae** | | |
| *Pachyhalictus burmanus* | 2 on sweat contaminated vegetation and on *Paraboea* sp. (Gessneriaceae), not attracted to flower | Too small to acquire pollen |

Dixon 1959; Bombosch 1962; Volk 1964; Peschken 1965; Budenberg & Powell 1992; Scholz & Poehling 2000; Sutherland *et al.* 2001; Verheggen *et al.* 2008; Stökl *et al.* 2010). Although there is discordance on some aspects, these authors agree that oviposition is not visually but olfactorily induced, whereas Shi *et al.* (2006, 2008) did not consider olfactory deception but proposed the dots as dummy aphids eliciting oviposition. Yet, despite this, one feature seems important to us. We think there is indication that there might be two types of brood-site deceptions. In the direct and more advanced type, entrapment is the direct cause of oviposition, after a volatile allomone released on or near the staminode attracted the pollinator there. In the indirect and more primitive type, as found in *P. dianthum*, the allomone is not released at this vantage-point but elsewhere on the flower. After alighting and ovipositing there, the pollinator has to fly to the staminode attracted by some other cue, before it will be entrapped. In fact, there may be a «latent» brood-site deception in many *Paphiopedilum*, but the allomone may be too weak or not sufficiently mimetic to elicit oviposition, though attractive enough for flies to alight. Lack of additional cues, e.g. tactile or gustatory, could also play a role. A weak brood-site deception

Tab. 10. Dimensions of pollinators of *Paphiopedilum thaianum* (t), *P. niveum* (n), *P. concolor* (c), and *P. godefroyae* (g).

| Pollinator species | Orchid species | Number of specimens measured | Thorax height (mm) | Body length (mm) |
|---|---|---|---|---|
| In the wild | | | | |
| *Lasioglossum orchidodeceptum* Pauly & Bänziger | t | 6 | 1.5-1.7 | 6.3-7.0 |
| *Tetragonula testaceitarsis* (Cameron) | n | 7 | 1.7-1.9 | 3.9-4.7 |
| *Eumerus figurans* Walker | c | 6 | 2.1-2.5 | 6.1-8.0 |
| *Eumerus nicobarensis* Schiner | c,g | 3 | 2.1-2.5 | 7.7-8.2 |
| In garden habitat | | | | |
| *Eumerus splendens* Wiedemann | g | 3 | 2.3-2.5 | 8.0-8.8 |
| *Graptomyza brevirostris* Wiedemann | g | 4 | 2.3-2.4 | 6.0-6.7 |
| *Syritta orientalis* Macquart | g | 5 | 1.9-2.4 | 7.1-8.7 |

additional to a predominant food-deception had been proposed for *P. villosum* (Bänziger 1996), and *P. parishii* may be similar. Brood-site deception can be suspected whenever a very strong female pollinator bias is found in deceptive pollination syndromes involving flies. Yet which type of deception occurs in myiophilous *Brachypetalum* is not clear because not only the young, but also adult milesiines tend to feed on decomposing plant matter.

It is interesting to note that the shift from melittophily in basal *Paphiopedilum* to myiophily in advanced ones has also occurred in *Cypripedium*, albeit to a minor degree, at a much later stage and to a different dipterous family. Ren *et al.* (2011) found *C. fargesii* pollinated by *Agathomyia* flies (Platypezidae). The orchid is one of seven species belonging to Section *Trigonopedia*, the most advanced *Cypripedium* (Cribb 1997), with non-typical flowers for the genus. On the other hand, we regard myiophily (and cantharophily) in two more basal *Cypripedium* as not convincingly substantiated. Pollen acquisition from nearctic *C. reginae* Walt. by one beetle and two syrphids is rather unusual and since it was the result of a mere 8 hours of flower watching (Vogt 1990), we consider it unreliable, probably accidental. Zheng *et al.* (2011) proposed mixed pollination in *C. flavum* by bumblebees (Apidae) and blowflies (Calliphoridae). Eight *Bombus* alighted on the flowers, of which 4 (50 %) entered the labellum and 4 (50 %) acquired pollen; for blowfly *Calliphora vomitoria* (L.) the counts were 203, 20 (9.9 %) and 7 (3.5 %). They concluded that bees were more efficient pollinators but that flies, being more frequent, pollinated more flowers. However, they overlooked that pollination is a two-step process, and when such low entrapping and pollen acquisition rates occur, evaluation must include both steps. Thus, since less than 10 % of the flies entered the first labellum, the chance that a fly carrying pollen (3.5 %) will enter a second flower to accomplish pollination is less than one of the 203 specimens in their study: so no pollination was to be expected. Further, persistently high populations of *C. vomitoria* at the flowers during two years of observations is unusual. Whereas adult blowflies are known to visit flowers for nectar (e.g. Kugler 1970), *C. vomitoria* are obligatorly necro- or coprophagous for reproduction (e.g. Tumrasvin *et al.* 1976; Wyss & Cherix 2006), food sources for which are highly ephemeral in nature (Beaver 1984). Consequently, it is likely that the flies came from garbage dumps or latrines in the area (may be up to several 100 m distance, probably unnoticed by the authors). As a synanthropic fly it has low populations in the wild except sporadically, when and where a large animal happens to die. Therefore the orchids were not in a natural (wild) environment with respect to the flies. Further, Zheng *et al.* (2011) did not elaborate on the real cause why the same blowfly species was able to leave by the exit of *C. flavum* in N Sichuan but perished in the pouch of this (and *C. yunnanense* Franch.) in Yunnan (Bänziger *et al.* 2008). The real reason is that the exit gap in northern flowers was nearly double in size, viz. 5.9–6.8 mm (Zheng *et al.* 2011) against 3–3.5 mm in the southern ones – wide enough in the former but too narrow in the latter for the flies to leave. In Yunnan the pollinator was a smaller bee, *Andrena orchidea* Scheuchl, not known from the north. We also note that Zheng *et al.* (2011) misquote Bänziger *et al.* (2008) that blowflies «accidentally removed and transported pollen» (in Yunnan). None did: those which pushed themselves as far as the anthers perished there glued to the narrow exit by the sticky pollen and additionally hindered from backing down by their strong backward-directed bristles (pp. 58–60, 62). We conclude that the northern populations of *C.*

Tab. 11. Dimensions of visitors on or near *Paphiopedilum thaianum* (t), *P. niveum* (n), *P. concolor* (c), and *P. godefroyae* (g).

| Visitor species | Orchid species | Number of insects measured | Thorax height (mm) | Body length (mm) |
|---|---|---|---|---|
| *Allograpta robinsoni* (Curran) | c | 4 | 1.9-2.5 | 7.4-7.7 |
| *Amegilla* sp. | t,c,n | 2 | 4.2-4.5 | 12-13 |
| *Apis cerana* Fabricius | t,c | 2 | 3.3-3.5 | 10.5 |
| *Apis florea* Fabricius | t | 2 | 2.4 | 8.3-8.7 |
| *Asarkina consequens* Walker | c | 2 | 3.9-4.3 | 13.0-15.0 |
| *Braunsapis hewitti* (Cameron) | c | 3 | 1.5-1.8 | 4.8-6.6 |
| *Ceratina chiangmaiensis* Warr., Mich. & Lekp. | c | 1 | 1.5 | 6.4 |
| *Ceratina lieftincki* v. d. Vecht | c | 1 | 1.6 | 6.9 |
| *Ceratina (Ceratinidia)* sp. | n | 0 | Not collected, | but rather large |
| *Ceratina (Neoceratina)* sp. 1 | t,n | 3 | 0.9 | 3.6-4.0 |
| *Ceratina (Neoceratina)* sp. 2 | g | 1 | 0.9 | 3.9 |
| *Clitellaria* sp. | c | 1 | 4.0 | 10.3 |
| *Dideopsis aegrota* (Fabricius) | c | 2 | 2.8-3.9 | 10.6-13.9 |
| *Episyrphus alternans* (Macquart) | c,t | 3 | 2.3-2.8 | 8.3-11.5 |
| *Eumerus aeneithorax* Brunetti | c | 3 | 1.8-2.1 | 6.7-8.7 |
| *Eumerus aurifrons* Wiedemann | c | 4 | 1.6-2.2 | 5.6-7.5 |
| *Eumerus nicobarensis* Schiner | t | 1 | 2.1-2.5 | 7.0 |
| *Eumerus rufoscutellatus* Brunetti | n,c | 5 | 3.2-3.9 | 12.2-12.8 |
| *Graptomyza brevirostris* Wiedemann | c | 4 | 2.3-2.4 | 6.0-6.7 |
| *Heterotrigona apicalis* (Smith) | t,c | 2 | 2.4-2.5 | 7.2-8.3 |
| *Heterotrigona melanoleuca* (Cockerell) | c | 2 | 2.6-2.9 | 6.3-6.7 |
| *Homalictus latitarsis* (Friese) | c | 3 | 1.4-1.5 | 5.1-5.4 |
| *Hoplonomia punctulata* (Dalla Torre) | n | 1 | 3.3 | 10.5 |
| *Hypopygiopsis infumata* (Bigot) | c | 1 | 5.9 | 14.0 |
| *Idiella mandarina* (Wiedemann) | t,n,c | 1 | 2.4 | 6.6 |
| *Isomyia*, 5 species | c | 10 | 4-5 | 10-12 |
| *Isomyia*, 1 species | n | 1 | 2.8 | 7.2 |
| *Lasioglossum albescens* (Smith) | c | 3 | 2.0-2.2 | 7.8-8.2 |
| *Lasioglossum perihirtulum* (Cockerell) | c | 2 | 1.4 | 5.6 |
| *Lasioglossum* cf. *salwinicum* (Blüthgen) | c | 1 | 1.5 | 5.9 |
| *Lasioglossum* sp. 1 | c | 1 | 1.5 | 5.6 |
| *Lasioglossum* sp. 2 | c | 1 | 1.5 | 5.3 |
| *Lasioglossum* sp. 3 | c | 1 | 1.7 | 5.9 |
| *Lasioglossum* sp. 4 | c | 1 | 1.6 | 5.9 |
| *Lasioglossum* sp. 5 | c | 1 | 1.5 | 6.0 |
| *Lasioglossum* sp. 6 | c | 2 | 1.1-1.4 | 5.6-6.1 |
| *Lepidotrigona doipaensis* (Schwarz) | c | 2 | 1.6-1.8 | 4.6-4.9 |
| *Lepidotrigona flavibasis* (Cockerell) | c | 2 | 1.7 | 4.4-4.6 |
| *Lepidotrigona nitidiventris* (Smith) | c | 2 | 2.4-2.6 | 6.3-6.8 |
| *Lepidotrigona terminata* (Smith) | t,c,n | 3 | 2.0-2.1 | 5.9-7.0 |
| *Lisotrigona cacciae* (Nurse) | t,g | 2 | 0.9 | 2.4-2.5 |
| *Lisotrigona furva* Engel | t | 2 | 1.1-1.2 | 3.0-3.2 |
| *Pachyhalictus burmanus* (Blüthgen) | n,c,g | 2 | 1.7 | 5.9-6.7 |
| *Pachyhalictus reticulosus* (Dalla Torre) | c | 2 | 1.6 | 6.1-6.8 |
| *Paragus* sp. nr. *politus* Wiedemann | c | 1 | 1.2 | 4.8 |
| *Pariotrigona klossi* (Schwarz) | t,n | 2 | 1.0 | 2.8-3.0 |
| *Pithitis* sp. | c | 1 | 1.8 | 7.2 |
| *Stomorhina discolor* (Fabricius) | c | 4 | 2.0-2.7 | 5.3-6.7 |
| *Tetragonula fuscobalteata* (Cameron) | t,g | 2 | 1.1-1.2 | 3.0 |
| *Tetragonula laeviceps* (Smith) | t,n,c,g | 3 | 1.4-1.5 | 3.7-4.1 |
| *Tetragonula* cf. *minangkabau* (Sakag. & Ino.) | t | 2 | 1.5 | 3.1-3.7 |
| *Tetragonula sirindhornae* (Mich. & Boong.) | t | 2 | 1.7-1.8 | 4.8-5.2 |
| *Tetragonula testaceitarsis* (Cameron) | t,c | 7 | 1.7-1.9 | 3.9-4.7 |

*flavum* had evidently adapted to larger-sized pollinators, bumblebees, well-known to predominate in colder climates (Michener 2000; Sugiura *et al.* 2002), where blowflies at best were rare accidental pollinators of *C. flavum*. This species, therefore, should be regarded as melittophilous only.

Seidenfaden's (1972) and Cribb's (1998) view that *P.* x *ang-thong* Fowlie is unlikely to be the natural hybrid between *P. godefroyae* and *P. niveum* proposed by Fowlie (1977), is supported by our findings because vector-wise the putative parents are incompatible, myiophilous and melittophilous, respectively. On the other hand, natural hybridization between *P. concolor* and *P. godefroyae* cannot be excluded since one of the pollinators of *P. concolor*, albeit a minor one, is in common with *P. godefroyae*. Although *P. concolor* grows north and *P. godefroyae* south from each other, they have been reported from the same province, Prachuab Khirikhan, S Thailand, though never at the same sites. Nevertheless, at least in Palaearctic regions, many syrphid species regularly migrate in large numbers over wide areas (Aubert & Goeldlin de Tiefenau 1981) and, as shown for *P. villosum*, pollen in slipper orchids can remain viable for two months (Bänziger 1996).

Our study supports the distinction of *P. thaianum* and *P. niveum* as two species. Superficially they may differ little but so do other slipper orchids accepted as good species, e.g. *P. bellatulum* and *P. godefroyae*, *P. callosum* and *P. barbatum* (Lindl.) Pfitzer, or *P. parishii* and *P. dianthum* (Cribb 1998). Two characters in *P. thaianum* and *P. niveum* are of fundamental significance because they effect the reproductive isolation of the two orchids, at least in combination. The scent is different, qualitatively and quantitatively, presumably the main factor for attracting pollinators differing at family rank. The difference in exit gap size hinders cross-species pollination, as also noted by Iamwiriyakul (2006). A parallel case where pollination biology helped clarifying taxonomy is the proposed merger of *C. smithii* Schltr. as a synonym into the very similar *C. tibeticum* King ex Rolfe because, among other characters, they share the same pollinators (Li & Luo 2009). Most importantly, recent new data based on statistical morphology and molecular genetics (Pumikong 2012) supports *P. thaianum* as a good species. Nevertheless, should future evidence reduce *P. thaianum* to an infraspecific rank within *P. niveum*, the missing link theory would still hold. It would apply to a not yet fully speciated *P. niveum* with its two infraspecific taxa *niveum* and *thaianum*.

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