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RESEARCH ARTICLE

Carpenter Bees and the Orchid of a Princess: Natural Pollination of *Sirindhornia monophylla* in Thailand

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ABSTRACT: Research on the pollination of *Sirindhornia monophylla* (Collett & Hemsl.) H. A. Pedersen & Suksathan was carried out in W Thailand, 2010–2012. The orchid is a nectariferous, non-autogamous and self-compatible terrestrial. During 120 man-hours of flower watching, three species of *Ceratina* were found to be the main pollinators, viz. *C.* (*Ceratinidia*) *lieftincki* van der Vecht, *C.* (*C.*) *collusor* Cockerell, *C.* (*Pithitis*) *smaragdula* (Fabricius), males and/or females. *Braunsapis hewitti* (Cameron) was a minor pollinator. *Ceratina* acquired pollinia on their forehead and in some cases they subsequently deposited massulae on the stigma of other *S. monophylla* flowers. Three further species, viz. *Ceratina* (*Ceratinidia*) *accusator* Cockerell, *C.* (*C.*) *chiangmaiensis* W., M. & L. and *C.* (*C.*) *bryanti* Cockerell, did not acquire pollinia; but in these cases all pollen in the visited flowers had already been removed by previous pollinators. *Ceratina* belongs to family Apidae, subfamily Xylocopinae, tribe Ceratinini, whereas *Braunsapis* belongs to tribe Allodapini. Fruit set was nearly 50%. This is the first detailed account on the pollination of a *Sirindhornia* species, a recently described genus with three species, all included in the Thai redlist.

KEY WORDS: Apidae, *Braunsapis*, *Ceratina*, Orchidaceae pollination, *Sirindhornia*, Xylocopinae.

INTRODUCTION

The genus *Sirindhornia* H. A. Pedersen & Suksathan, named after H.R.H. Princess Maha Chakri Sirindhorn of Thailand, was described in 2003; it belongs to subfamily Orchidoideae, tribe Orchideae, subtribe Orchidinae and accommodates three terrestrial species that occur in open limestone habitats at 800–2200 m altitude (Pedersen et al., 2003). *Sirindhornia mirabilis* H. A. Pedersen & Suksathan and *S. pulchella* H. A. Pedersen & Indham. are narrow endemics from northern Thailand, whereas *S. monophylla* (Collett & Hemsl.) H. A. Pedersen & Suksathan is more widespread; its only population in Thailand is sympatric with *S. mirabilis*. All three species are included in the National Thai redlist (Santisuk et al., 2006) – *S. monophylla* being classified as "rare" (R), the other two species as "endangered" (EN). Srimuang et al. (2010a, 2010b) provided comprehensive information on aspects of demography, recruitment, breeding system, flowering phenology, male and female reproductive success and patterns of fruit set in all three species. In contrast, very little and fragmentary information on their pollination biology has been published up to now (Srimuang et al., 2010a; Watthana et al., 2013). This is a serious gap, since knowledge of the pollination biology of individual orchid species is widely acknowledged as being highly important for their long-term conservation (Roberts, 2003; Pemberton, 2010). In this paper, we contribute to fill the information gap for *S. monophylla*.

Sirindhornia monophylla (Fig. 1) is fully self-compatible, but non-autogamous, as demonstrated experimentally by Srimuang et al. (2010a). Consequently, it depends on pollinators for fruit production in its natural habitat. With its zygomorphic, more or less horizontal, mainly white to purple flowers that exude nectar hidden in a spur and offer an enlarged lip as a landing platform (provided with tufts of coloured papillae that serve as nectar guides), the species fits the bee pollination syndrome of van der Pijl and Dodson (1966). In the study covered by this paper, we attempted: (1) to identify its legitimate pollinators, (2) to reveal the pollination mechanism and (3) to observe and describe the behaviour of pollinators in relation to *S. monophylla*. This is the full paper underlying an oral presentation given by K.S. at The 8th International Symposium on Diversity and Conservation of Asian Orchids, held in Shenzhen, China in 2012 (abstract: Srimuang et al., 2013).

MATERIALS AND METHODS

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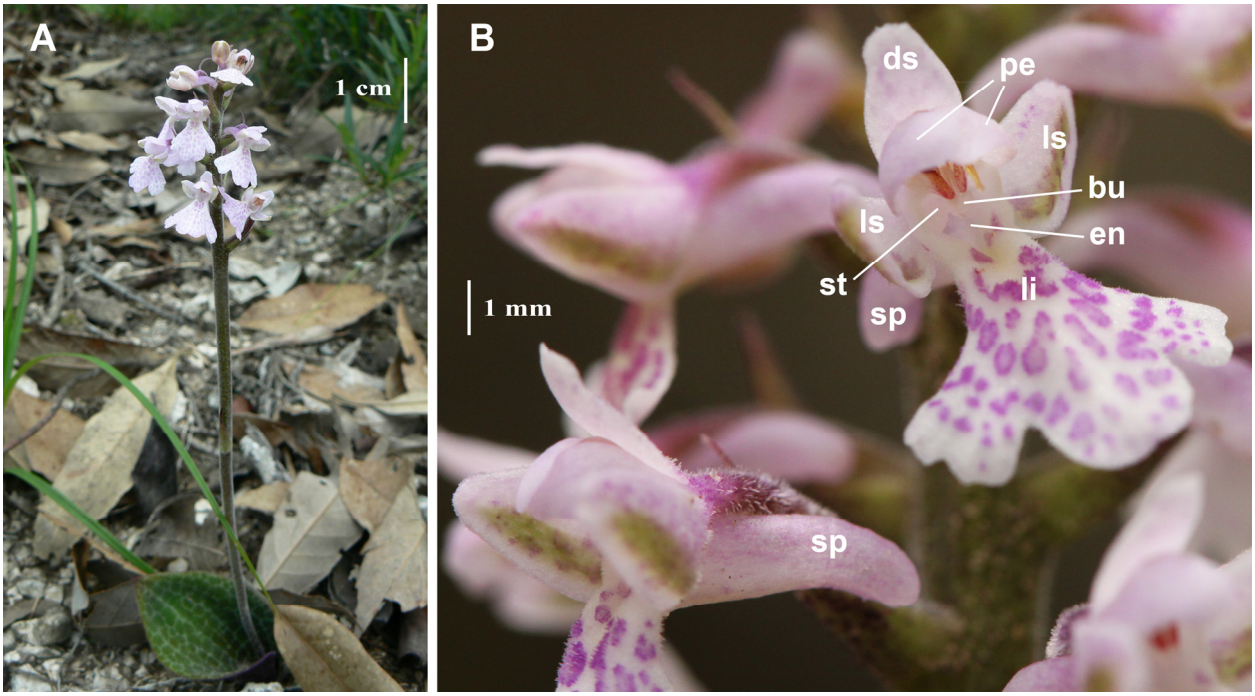


Fig 1. Morphology of *Sirindhornia monophylla*. A: Habit. B: Floral morphology (anther largely hidden by the petals). Abbreviations: bu, bursicle; ds, dorsal sepal; en, entrance of spur; li, lip; ls, lateral sepal; pe, petals; sp, spur; st, stigma. Photos by K. Srimuang.

Functional morphology of the flower

The inflorescence (Fig. 1A) measures 5–14 cm in length on a peduncle of 7–26 cm, and bears 11–68 individual flowers (improved data from previous findings; Srimuang et al., 2010a). The flower (Fig. 1B) is 0.8–1.2 cm in diameter, white to pale rose with numerous tufts of purple papillae on the lip. In the resupinate flower with incurved sepals and petals, the lip (offering a landing platform) measures 3.4–6.8 × 4.1–8.4 mm. It is more or less 3-lobed in its distal part and provided with a basal, nectariferous spur that is nearly cylindrical, somewhat downcurved, 4.5–7.7 mm long and 0.8–1.8 mm in diameter at the entrance. Glucose content of the nectar is approximately 5–10 mg/ml. The straight to slightly recurved column is 1.5–2.8 mm long and provided with a subterminal, erect, 2-loculate anther and a concave stigma on its lower front. The rostellum is porrect and then strongly recurved (in a knee-like bend) to form a narrow fold between the anther locules; the knee-like bend forms a single 2-loculate bursicle that is narrowly hinged at its lower margin. The pollinarium consists of two separate hemipollinaria, each composed of a basitonous, clavate pollinium and a minute viscidium, the latter being completely hidden in the bursicle. Each pollinium is composed of a long, sterile caudicle at base and a fertile distal part where the pollen grains are assembled in numerous, loosely attached massulae.

Flowering phenology

The flowering season lasts from mid-May to early July, with a peak from the end of May until mid-June. The longevity of individual flowers is approximately 3 weeks (but if pollinated, the flower withers in 3 days). Flowering starts from the bottom of the inflorescence and progresses to the top.

Study site and methods

The study was carried out at Umphang Wildlife Sanctuary, Tak Province, W Thailand. The habitat was craggy limestone mountains approximately 800–1,000 m a.s.l. The plants grew in grassy patches on slopes covered by open forest with *Strobilanthes* spp. (Acanthaceae); *Onosma burmanicum* Collett and Hemsley (Boraginaceae); *Leptodermis crassifolia* Collett & Hemsl. (Rubiaceae); *Quercus helferiana* A. DC. (Fagaceae) and *Buxus* sp. (Buxaceae) as dominant species. Population density of flowering plants of *Sirindhornia monophylla* per area under observation (mostly 2 by 3 meters) was 3–5. A total of c. 20 flowering individuals were kept under observation for pollinator visits.

Pollination behaviour was recorded by field notes, photographs and videos (by K.S.). When observing the orchids from some distance (3–5 m) in order to reduce possible human impact (body odours, visual distraction)on insect visitors, binoculars or monoculars

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were used. Observations were made from 27 May to 1 June 2010 (54 h, one person), 30 May to 2 June 2011 (24 h, one person) and 31 May to 2 June 2012 (42 h, two persons). The observation time was from 8:30 AM until 5:00 PM, with a total of 120 man-hours watching time.

It soon became clear that the main pollinators were small carpenter bees (*Ceratina* spp.), cf. the Results section below. Generally, only those *Ceratina* bees that settled on *S. monophylla* flowers were collected; collecting all *Ceratina* that approached the flowers would have reduced the chance of pollination. This, however, prevented exact identification of *Ceratina* which did not settle on the flowers and, hence, the frequency of the various species in the habitat. Insects were collected by net or a plastic box held over the flower/inflorescence, and subsequently euthanized by ethyl acetate. In *S. monophylla* successful removal and deposition of pollinia by the pollinator depend on its appropriate head width – if too small the head will not touch the anther, if too large it cannot enter the flower to contact the anther. Head width in set specimens was measured by micrometer under a stereo microscope.

For the assessment of fruit set, four plots of 15–100 m^2 were selected which had the highest number of *S. monophylla* plants. These were inspected during three consecutive years (2010–2012), one month after the end of the flowering period. At this time, the pollinated flowers were clearly recognizable by the fully swollen ovary.

Taxonomic notes on the pollinators

Insects were identified by H.B. and vouchers deposited at the Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University (DEFACU). Identification of the difficult *Ceratina*, subgenus *Ceratinidia*, was based on the comprehensive review by Warrit (2007), and a recent addition Warrit et al. (2012). However, some of our specimens could not be definitely allotted to any of the species treated. It was not clear whether some of the (mostly small) differences, including the male terminalia, were due to within-species variations or to hitherto untreated species. Identification of *Ceratina*, subgenus *Pithitis*, was by the old treatment of van der Vecht (1952). Michener (2000) has upkept the subgeneric status of *Pithitis*. Distinction between *C.* (*P.*) *smaragdula* (Fabricius) and *C.* (*P.*) *unimaculata* Smith is reliable only in males. *Braunsapis hewitti* (Cameron) was identified by comparing it with specimens in the collection of H.B., originally identified by H. Dathe. All other insects were identified as mentioned in Bänziger et al. (2012).

RESULTS

Observations on pollinators

The main pollinators of *S. monophylla* were found to be small carpenter bees, subfamily Xylocopinae, tribe Ceratinini, viz. *Ceratina* (*Ceratinidia*) *lieftincki* van der Vecht, *C.* (*C.*) *collusor* Cockerell and *C.* (*Pithitis*) *smaragdula* (Fabricius) (Table 1, Fig. 2). *Braunsapis hewitti* (Cameron), an exponent of the tribe Allodapini, was a minor pollinator. However, three further species, viz. *Ceratina* (*C.*) *accusator* Cockerell, *C.* (*C.*) *chiangmaiensis* W., M. & L. and *C.* (*C.*) *bryanti* Cockerell, almost certainly are also legitimate pollinators. They failed to acquire pollinia when visiting the flowers, but in these cases all pollen in the visited flowers had already been removed by previous pollinators.

Insect activity was mainly from 10:00 AM until 4:00 PM. Pollinators tended to circle around the inflorescence or approached it in a zig-zag manner before flying straight to, and landing on, a lip (Fig. 2A), possibly visually attracted to the numerous tufts of purple papillae functioning as nectar guides. Generally, they crawled around, up and down, the flower. They then often flew off, but about one in ten entered the central interior part of the flower (i.e. the concave space in front of the column, bounded by the incurved sepals and petals and the base of the lip), see Fig. 2C. Here, they presumably inserted the proboscis into the spur in order to suck nectar – the uncertainty is because the frontal part of the head was concealed inside the flower (Fig. 2C) and the sequence brief (2–5 s). As they retreated from the central interior part of the flower, in about half the cases they hit the rostellum exposing the viscidia which glued onto the clypeus, labrum, and/or the paraocular area of the forehead (Fig. 2B, D & E). In the remaining cases, they flew off without (hemi) pollinarium. Some of the individuals carrying a pollinarium would instantly fly away out of view, possibly startled by the experience of getting a pollinarium glued to the forehead. Some, however, seemed to be unaffected and crawled onto nearby flowers (Fig. 2B), or flew around the same or a nearby inflorescence where the same sequence might be repeated. The pollinaria attached to the pollinators' head were consistently directed forwards (Fig. 2B). So, as the bee entered another flower to suck nectar, the pollinia struck the stigma, depositing variable numbers of massulae, but not entire pollinia.

Head widths of *S. monophylla* pollinators and some other flower-visiting insects from the same habitat are shown in Table 2. The minimum and maximum head widths that would enable a visitor to function as pollinator were found to be 1.0–1.2 mm and about 2.5 mm, respectively.

Fruit set

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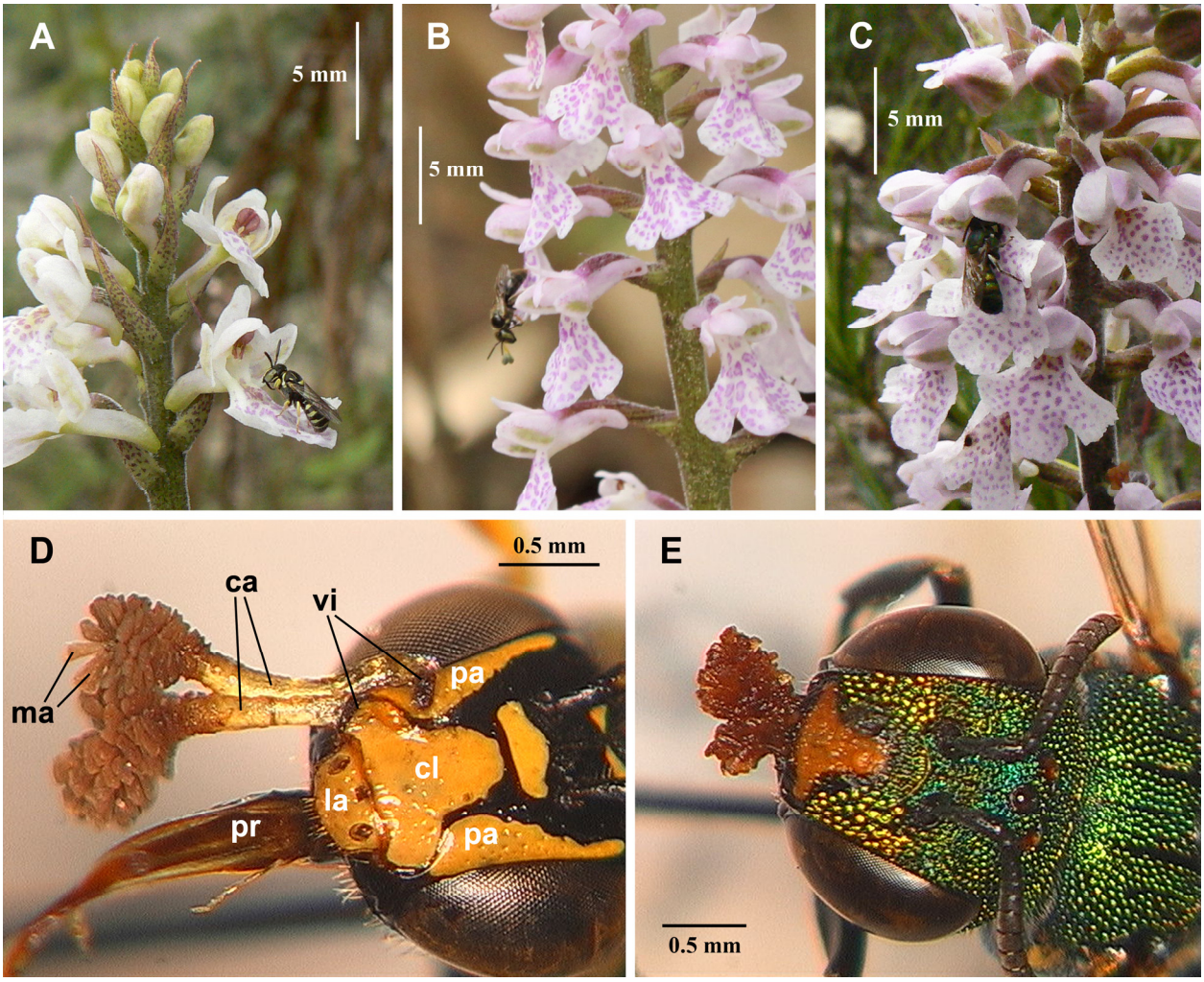


Fig. 2. Examples of pollinators of *Sirindhornia monophylla* (A–C, visiting the orchid at our study site; D–E, set specimens). A: *Ceratina* (*Ceratinidia*) sp. positioned on the lip before entering the interior of the flower. B: *Ceratina* (*C.*) sp. crawling on the flowers, probably in search of nectar; note the just acquired pollinarium, glued to the bee's forehead and characteristically directed forwards. C: *Ceratina* (*Pithitis*) *smaragdula* completely entering the interior of the flower an instant before acquiring a pollinarium (cf. E). D: Forehead of male *Ceratina* (*C.*) *lieftincki* with a pollinarium of *S. monophylla* stuck to the right paraocular area of the head (photo taken 6 months after capture). E: Forehead of male *Ceratina* (*P.*) *smaragdula* with a pollinarium of *S. monophylla* stuck to the clypeus (same individual as in C, but photographed two years after capture, hence the collapsed and greasy appearance of the pollinarium). Abbreviations: ma, massulae; ca, caudicles; cl, clypeus; la, labrum; pa, paraocular area; pr, proboscis; vi, viscidia. Photos by K. Srimuang (A–C) and H. Bänziger (D–E).

The uniloculate capsules were sessile, spreading, slightly incurved, fusiform, 18–22 mm long, 3–4 mm in diameter, thickest below the middle, papillose-pubescent and with 6 longitudinal furrows. The flower production and natural fruit set observed during the study period are surveyed in Table 3. The three-year average of relative fruit set was 48.5%.

DISCUSSION

Although only few pollen acquisitions and depositions were observed, viz. 6 and 5, respectively (Table 1), from the following evidence there is little doubt that the four species of small carpenter bees, *C.* (*C.*) *lieftincki*, *C.* (*C.*) *collusor* and *C.* (*P.*) *smaragdula*, and *B. hewitti*, males and/or females, are legitimate pollinators of *S. monophylla*; three additional *Ceratina* species did not acquire pollinia because they visited pollen-depleted flowers. The bees are all closely related, except the minor pollinator *B. hewitti*. Their head size (Table 2) is consistently within the range that enables access to the central interior part of the flower. In *S. mirabilis*, the same group of pollinators was found (Srimuang et al., unpublished). Low pollinator frequency is not uncommon in orchids. In *Paphiopedilum charlesworthii* (Rolfe) Pfitzer only two pollinators were seen acquiring pollen during 218 h of flower-watching over six years (1992–1996), which

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Table 1. Confirmed and almost certain pollinators of *Sirindhornia monophylla* (all belonging to family Apidae, subfamily Xylocopinae). Plain numbers: number of individuals which entered a flower; in parentheses: number of pollen acquisitions; in brackets: number of pollen depositions.

Pollinator species	Females	Males
Ceratinini		
Ceratina (*Ceratinidia*) *lieftincki* van der Vecht	3 (0) [0]	8 (2) [2]
Ceratina (*Ceratinidia*) *collusor* Cockerell	3 (1) [1]	0 (0) [0]
[1]*Ceratina* (*Ceratinidia*) *accusator* Cockerell	1 (0) [0]	0 (0) [0]
[1]*Ceratina* (*Ceratinidia*) *chiangmaiensis* W., M. & L.	1 (0) [0]	0 (0) [0]
[1]*Ceratina* (*Ceratinidia*) *bryanti* Cockerell	1 (0) [0]	0 (0) [0]
[2]*Ceratina* (*Pithitis*) *smaragdula* (Fabricius)	1 (?) [0]	3 (2) [2]
Allodapini		
Braunsapis hewitti (Cameron)	2 (1) [0]	0 (0) [0]

[1] No pollinia aquired because they were already removed by a previous pollinator.
[2] One additional specimen acquired pollinia but escaped collection when it rapidly left the flower, so its sex could not be established.

accords well with the extremely low fruit set found, viz. 0.86% in 15–466 flowers investigated yearly over 11 years (1992–2002) (Bänziger, 2002 and unpublished). Two other examples are *Epipogium aphyllum* Sw. (Claessens and Kleynen, 2011) and *Luisia curtisii* Seidenf. (Pedersen et al., 2013). Pollinators were not common in the habitat of *S. monophylla* and were widely outnumbered by other flower-visiting insects which rarely visited *S. monophylla*, unlike *S. mirabilis* (Srimuang et al., unpublished). In the same type of habitat, but 4 km from the *S. monophylla* site, in the vicinity of *P. concolor* (Bateman) Pfitzer, 42 species of flower-visiting insects were seen (26 Hymenoptera, 16 Diptera) (Bänziger et al., 2012), about 20 of which would have been of suitable size for entering flowers of *S. monophylla*. To them, *S. monophylla* evidently was not attractive enough. In most cases, non-pollinating visitors just briefly circled around the inflorescence without landing, only rarely settling on it for a short while.

Srimuang et al. (2010b) hypothesized that one *Sirindhornia* pollinium can successfully pollinate several flowers as its distal, fertile end consists of loosely assembled massulae that easily break off (Fig. 2D). That hypothesis is in agreement with previously reported observations on species of other genera having sectile pollinia and similarly belonging to subtribe Orchidinae s.l. (e.g. Darwin, 1862; Neiland and Wilcock, 1995; Claessens and Kleynen, 2011), and it was confirmed for *S. monophylla* in the present study. This phenomenon may greatly reduce the high rates of full sibness potentially resulting from the unequal male (and female) contributions of individual *S. monophylla* plants that were demonstrated by Srimuang et al. (2010b).

The circumstance that pollinia attached to the pollinators' head pointed forwards already from the moment they were extracted from the anther is unusual within the Orchidinae. Thus, already Darwin (1862) demonstrated how pollinia acquired from selected members of this subtribe are first erect, but gradually pivot forwards or sidewards, meaning that they do not reach a position fitting into the fertile stigma until several seconds or minutes have passed – thus reducing the probability of autogamy and geitonogamy. For a survey of the "bending times" reported for caudicles in European Orchidinae, see Claessens and Kleynen (2011).

The level of natural fruit set in *S. monophylla* observed during the three years of this study was of the same magnitude as reported for the same population for 2006 and 2008 (Srimuang et al., 2010a, 2010b). Furthermore, it is well within the usual range reported for rewarding orchid species in general (cf. Neiland and Wilcock, 1998; Tremblay et al., 2005; Scopece et al., 2010). These features in combination suggest that the pollination system of our study population is stable and well-functioning. In subtribe Orchidinae, both rewarding (nectariferous) and deceptive taxa are widespread, and pollination systems appear to have shifted on numerous occasions during the last 23 million years (Inda et al., 2012). Both male and (especially) female reproductive success are generally higher in the rewarding taxa (Scopece et al., 2010).

The previously reported occurrence of the natural hybrid *S. mirabilis* × *monophylla* at our study site (Pedersen and Ormerod, 2009) demonstrates that the parental species share one or more pollinator species, at least occasionally. In contrast, the nectarless *Ponerorchis chusua* (D. Don) Soó – possibly a close relative of *Sirindhornia* – is pollinated by bumblebees

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Table 2. Head width (mm) of confirmed and almost certain pollinators of *Sirindhornia monophylla,* and some other flower-frequenting insects in the same habitat.

Taxon	Head width
HYMENOPTERA	
APIDAE, Xylocopinae	
Allodapini	
Braunsapis hewitti (Cameron)	1.43–1.78
Ceratinini	
Ceratina (*Ceratinidia*) *accusator* Cockerell	1.63–1.78
Ceratina (*C.*) *bryanti* Cockerell	1.78–1.90
Ceratina (*C.*) *chiangmaiensis* W., M. & L.	1.73
Ceratina (*C.*) *collusor* Cockerell	1.42–1.94
Ceratina (*C.*) *lieftincki* van der Vecht	1.65–2.33
Ceratina (*Neoceratina*) sp.	1.23–1.45
Ceratina (*Pithitis*) *unimaculata* Smith	2.15
Ceratina (*P.*) *smaragdula* (Fabricius)	1.88–2.31
HALICTIDAE	
Lasioglossum sp. E*	2.0
DIPTERA	
SYRPHIDAE, Milesiinae	
Eumerus rufoscutellatus Brunetti	3.5

***: "E" designates one of five unidentified *Lasioglossum* species found at the study site.**

(*Bombus* spp.; Sun et al., 2011).

In most genera of subtribe Orchidinae, pollination by bees is predominant (van der Cingel, 2001; Pridgeon et al., 2001; Claessens and Kleynen, 2011), but up to now species of *Ceratina* have only been reported to contribute to pollination in species of *Serapias* (Claessens and Kleynen, 2011 and references therein). Indeed, the general importance of *Ceratina* for orchid pollination appears to be very minor, since additional records of orchids pollinated by representatives of this genus are limited to *Cypripedium parviflorum* Salisb. (Cypripedioideae; Stoutamire, 1967, sub nom. *C. calceolus*) and *Nervilia* (Epidendroideae; Pettersson, 1989). Nevertheless, a few species of *Ceratina* (and one of the genus *Braunsapis*) have now been documented to be of crucial importance for the pollination and, hence, the long-term survival of *Sirindhornia monophylla*.

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Table 3. Flower production and fruit set in *Sirindhornia monophylla* at the study site in Umphang Wildlife Sanctuary, Thailand, 2010–2012.

Year	N_{inflor}	$N_{flowers}$	N_{fruits}	% Fruit set
2010	18	378	220	58.9
2011	18	401	158	42.0
2012	15	342	127	44.7

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木蜂與公主蘭：探討泰國 *Sirindhornia monophylla* 的自然授粉

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摘要：本文研究了泰國西部*Sirindhornia monophylla*的授粉生物學。此種蘭花為可分泌花蜜、非自花授但自交親合的陸生蘭。在經過了120個工時的實驗觀察後，有三個花蘆蜂屬的物種被視為主要的授粉者，分別是*Ceratinidia lieftincki*、*C. collusor*和綠蘆蜂，雄性與雌性都有授粉的行為；何威布朗蜂則為次要的授粉者。花蘆蜂會將花粉置於前額，並在拜訪下一朵公主蘭時將花粉塊沾黏於其柱頭上。另外有三種花蘆蜂屬的授粉者雖然也會拜訪花朵，但由於這些被拜訪的花朵其花粉都被上一個授粉者給帶走，因此並沒有觀察到這三種花蘆蜂屬的授粉者帶走花粉塊的行為，這額外的三個物種分別是：*C. accusator*、*C. chiangmaiensis*和*C. bryanti*。本研究是首次對*Sirindhornia*屬物種的授粉研究，此屬下的三個物種都在泰國紅皮書名單中。

關鍵詞：蜜蜂科、蘆蜂屬、花蘆蜂屬、蘭科授粉、*Sirindhornia*、Xylocopinae。

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