POLLINATION OF A FLOWERING ODDITY: *RHIZANTHES ZIPPELII* (BLUME) SPACH (RAFFLESIACEAE)

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ABSTRACT

In a pollination syndrome based mainly on brood-site deception, female carrion flies *Lucilia porphyrina, Chrysomya pinguis, C. chani* and *C. villeneuvei* are *R. zippelii*'s main pollinators among a further six scarce/potential calliphorid (Diptera) pollinator species. A 'stuffy room' and a weaker excrement-like odour attract flies presumably from dozens of meters; at close range fleshy colours and a tangle of hairs probably dissimulate a mammal carcass, orifices and/or wounds. Pollinators are lured down the hairy tube towards the circumambulator which is mistaken for an oviposition cavity. Entering the circumambulator requires intrusion through the annular gap topped by the ring of anthers from which pollen mush is smeared onto the flies' back. More pollen is acquired at the gap on leaving the circumambulator. The mush then clots and hardens while keeping some germinability for 2–3 weeks. Pollen delivery on a female flower is analogous, the clot being readily reliquefied and 'sponged' off by the fluid-soaked papillae of the stigma. Flies may act as long distance pollinators as they are strong flyers (50 km/week) and long-lived (4–7 weeks). 50% of the flowers were oviposited upon by up to a thousand eggs whose hatchlings die of starvation or ant predation. Very few males visited the flower where they sucked nectar (as females did) and/or mated but did not pollinate. Other non-pollinating visitors included 5 species of full dupes, 6 of half dupes, 12 of opportunists and 2 of 'parasites' belonging to 12 families of 5 insect orders.

INTRODUCTION

Rhizanthes Dumortier along with *Rafflesia* R. Brown and *Sapria* Griffith, is one of the three 'core' genera of the wholly parasitic family Rafflesiaceae. Compared to the flamboyance and fame of its two closest relatives, *Rhizanthes* is modest and reputedly even rarer. However, it outperforms them with its perplexing aspect. To the few people who at dawn have seen the flower—which starts opening at midnight—it may resemble the spike-trap of a carnivorous plant. In full bloom it is more like a starfish or medusa, while its central parts remind one of the blood-shot orifice of a hairy mammal.

Behind this disconcerting look hide potent insect-manipulating powers to entice, appease and deceive a disparate cohort of nectar thieves, opportunists, female-chasing males and predators as well as dupes which lay hundreds of ill fated eggs on the flower. In a comprehensive review of parasitic flowering plants, KUIJT (1969) jokingly called *Rafflesia* the 'prima donna' of all parasitic plants. For *Rhizanthes* the corresponding epithet might be 'Rasputin'.

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Received 1 March 1996; accepted 1 June 1996.

MEIJER & VELDKAMP (1988) reviewed in detail our state of knowledge of *Rhizanthes* giving data on its nomenclature, taxonomy, morphology and geographic distribution (e.g. BECCARI, 1869; SOLMS-LAUBACH, 1876, 1898; HEINRICHER, 1905; CAMMERLOHER, 1920). A recent study (BÄNZIGER, 1995) added new information, especially on the plant's virtually unknown ecology: population structure, bud and flower phenology, functional morphology, and ecology and morphology of the flower's newly discovered host. It was also shown that in *R. zippelii* (as in *Sapria* and *Rafflesia*) the pollen has unusual properties: exuded by the anthers as a mush, it dries and hardens once removed onto the back of a pollinator; it retains germinability in this state, progressively declining, for 2–3 weeks; and it is quickly reliquefied on contact with the fluid-soaked stigma. In addition, *R. zippelii's* geographic distribution, previously known only from Indonesia and Malaysia, has been extended to S Thailand. Finally, it was proposed that *R. lowi* (Beccari) Harms, 1868 should be synonymized with *R. zippelii* (Blume) Spach, 1827.

Before these recent studies virtually no field observations had been made on the pollination of *Rhizanthes*. Insects observed on the flower had been identified only as carrion flies, fruit flies, gnats, ants, etc. (e.g. FORBES, 1885; HEINRICHER, 1905; WINCKEL, 1918) with hardly a reference to their behaviour. No distinction was made between pollinators and mere visitors, an important difference because some opportunistic non-pollinators can be more frequent than the actual pollinators. Interestingly, MEIJER & VELDKAMP (1988), although aware that flies visit the flowers, suggested on cytological grounds that, unless there is a long delay between pollination and fertilization, the plant might reproduce asexually. HEINRICHER (1905) had already theorized that no pollen vectors may be involved, although he also suggested that small gnats are probably involved in the pollination.

Yet as early as 1868 DELPINO, whose comprehensive work on the pollination of flowering plants has all too often been forgotten, had attempted a first, purely theoretical, interpretation of the pollination mechanism. Based on BLUME'S (1827) figures he was misled into thinking that the crater of the ampulla was an entrance. Through this hole pollinators—which he correctly prophesized to be flies on account of the malodorous smell mentioned by Blume—would enter a cavity analogous to that of other flowers with a narrow entrance and a large floral cavity, e.g. such as found in the closely related Aristolochiaceae. As in these flowers, the flies would remain temporarily prisoners and enact pollination, until released when the flower dropped. Delpino, despite his often clairvoyant work, failed with his interpretation this time, obviously due to lack of plant material. Yet in the intervening 130 years to my knowledge no observations on actual pollination have been published on this flowering oddity.

STUDY AREAS

Observations were made at three sites in evergreen rain forest. The most northerly (site a) was in Sukhirin District, Narathiwat Province, S Thailand. The other two (sites b, c) were between Gopeng and Chenderiang, S Perak, Peninsular Malaysia, the general area mentioned by MOLESWORTH ALLEN (1968). The sites, together with habitat and microclimatic notes, including the time of studies in 1994 and 1995 (cf. also Tables 1–6),

have been described in some detail (BÄNZIGER, 1995).

INSECTS ASSOCIATED WITH *R. ZIPPELII*

Insects approach the flower for various reasons and may be directly or indirectly associated with it. For convenience the insect community involved is grouped into pollinators and non-pollinators which are further categorized. A third group tends to turn up in the flower's vicinity and may only occasionally settle on it. Among these are mate–seeking males of pollinators for which the flower is a rendezvous site. But for most the reason for this behaviour is not clear. Perhaps they are somehow attracted to the flower but not strongly or 'convincingly' enough to settle on it. The observer's own body odours also played a role in this since some of these flies settled on him and the objects he had contacted. This insect group included calliphorids such as *Isomyia delectans* Walker and syrphids like *Asarkina consequens* Walker, *Eristalis suturalis* Brunetti, *Graptomyza longirostris* Wiedemann.

I have not yet studied the behaviour of drosophilids which, although attracted at early anthesis, produce larvae which almost certainly thrive in old, decomposing flowers.

The various terms used for floral structures have been explained in my previous study on *R. zippelii (loc. cit.)*.

Pollinators

From behavioural evidence the main pollinators of *R. zippelii* are 4 species of blow flies or carrion flies (Calliphoridae, Diptera), with an additional 2 less common ones and 4 which are exceptional or potential pollinators. Only females were pollen vectors, although males sometimes settled on *R. zippelii*. No male was seen acquiring pollen or exhibiting any behaviour conducive to pollen acquisition. Baiting by faeces and rotten fish did not reveal a different calliphorid fauna at the sites although slightly more *Chrysomya megacephala* and *Lucilia papuensis,* besides more males in general, were attracted to baits than to *R. zippelii.*

In most cases it was possible to identify the calliphorid species without capturing them. However, distinction of *C. pinguis* from *C. chani* required collection for examination under magnification. Nevertheless, unless a fly was of particular interest, I desisted from collecting it in order to avoid disruption of the flies' behaviour. As a consequence *C. pinguis* and *C. chani* are lumped together in Tables 1–6. From the material captured on or near *R. zippelii* (67 *C. pinguis,* 14 *C. chani,* all sites, both years) the frequency breakdown is about 5 *C. pinguis* to 1 *C. chani.*

A more problematic species, *C. defixa* (Walker), can be distinguished from *C. pinguis* only by microscopic examination of the genitalia of the males which, unfortunately, are not pollinators. Because of this, and because the species so far has never been recorded in Thailand and W Malaysia (Wyatt, pers. comm.), the taxon is not further considered in this study.

Well over 900 calliphorid visits were recorded (Tables 1–6) (actual individuals were fewer because of revisitation) on 17 flowers during a total of over 140 h of flower watching

(about half in S Thailand).   More than 280 specimens were collected.

Main pollinator species

Lucilia porphyrina (Walker) (Figs. 7, 10)

With 411 sightings of the species on the flower this fly was the most common visitor. Furthermore, except for an occasional *Hypopygiopsis* sp., it was the earliest blow fly to arrive on the flower, long before pollen was depleted, generally by mid–afternoon. Despite this, *L. porphyrina* was less efficient at acquiring pollen than *C. pinguis* and *C. chani*, i.e., in 47 cases (about 17% of total visits before pollen depletion) against 61 cases (29%) of the latter two (considered together).   *L. porphyrina* is rather restless, more timid and, at least the early arrivals, less prone to enter the circumambulator.   Yet *L. porphyrina* may nevertheless be the most efficient pollinator because of its relatively high rate of re-visiting *R. zippelii*—a prerequisite for pollen delivery—as evident from flies arriving on the flower with pollen already sticking to its back, viz. 32 cases (7.7% of the species's total visits or 68% of successful visits).   In 12 (38%) of these cases the time interval must have been many hours or, most likely, one or more days judging from the solidified state of pollen loads.   The fly probably exhibits a higher degree of site fidelity than *C. pinguis* and *C. chani*, an assumption which seems to be corroborated by the early arrival at the flower compared with other *Chrysomya* species.   Eight males settled on the flower, generally only briefly, some sucking nectar, none entering the tube.

Chrysomya pinguis (Walker) and Chrysomya chani Kurahashi (Figs. 6, 9)

With 316 visits by these two species (theoretical frequency: 263 *C. pinguis* and 53 *C. chani*) to the flower, they were the second and third most common pollinators and the most efficient in acquiring pollen, viz. together 61 observed cases of pollen acquisition (about 29% of visits before pollen depletion).   They were less restless and more 'daring' in entering the circumambulator.   However, with only 8 returnees carrying pollen the species seem more dispersive and therefore may contribute less to pollen delivery than *L. porphyrina*. On the other hand, *C. pinguis* and *C. chani* may be better long distance pollen vectors. Twenty-two males landed on the flower; their behaviour was like that of *L. porphyrina*.

Chrysomya villeneuvei Patton (Fig. 8)

Forty-eight sightings of this species were noted.   It was missing at site (b) in both research years.   Six specimens acquired pollen (about 19% of visits before pollen depletion) and 4 specimens arrived with solid pollen.   General female behaviour was similar to that of *C. pinguis* but not so the males.   While some males sucked nectar, most used the flower as a rendezvous site.   They waited for females, suddenly grabbing one by getting on her back, the two then flying off slowly in tight grasp.   The same behaviour was also observed on *Rafflesia kerrii* Meijer (in prep.).   The fly's behaviour was somewhat unexpected as males of most blow flies use feeding sites and not oviposition sites for mating.   Feeding sites include 'ordinary' flowers like acacias (GUILLOT ET AL., 1978; MACKLEY & LONG, 1983), umbellifers, composits (STEINER, 1948; KUGLER, 1951) where males and females take nectar and pollen.

Chrysomya megacephala (Fabricius) (Fig. 1)

Nine visits with two pollen acquisitions were observed. The species was missing at site (b). Female and male behaviour was similar to that of *C. pinguis*. I found great numbers of the species on anthropogeneous effluvia and garbage at the outskirts of an Orang Asli village bordering the forest in the area of sites (b) and (c).

Hemipyrellia ligurriens (Wiedemann)

Only 5 specimens were seen in S Thailand, none in Malaysia. It was a very active fly which often entered the tube and circumambulator. One pollen acquisition was witnessed. Probably it is an efficient pollinator but too scarce to be of significance when compared to *L. porphyrina* and *C. pinguis*. No males were present.

Exceptional and potential pollinators

Hypopygiopsis infumata (Bigot) (Figs. 2, 4)

With 57 sightings this fly was the fourth most common calliphorid in S Thailand, but was scarce at Malaysian sites. Full-sized specimens are about double the size of *L. porphyrina* and are thus too large to penetrate the average–sized gap between anthers and furry hairs, although attempts to do so were frequent. Nevertheless, as in many Diptera, adults vary considerably in size so that the smallest are just half the largest individuals, i.e. comparable to *L. porphyrina*. Indeed two *H. infumata* successfully intruded into the circumambulator but no pollen was acquired solely because it was already depleted (cf. also Appendix 1). Males were also attracted to the flower but used it as a rendezvous site and also occasionally settled on the flower and sucked nectar. They lurked for hours in the vicinity, on leaves, twigs, or on the ground, every few minutes changing position by turning to the right or the left or flying to another vantage position near by, and dashing towards a female flying to or from *R. zippelii*. Unlike *C. villeneuvei*, males of this species seized females while airborne and flew off with them in tight grasp. They were among the earliest calliphorids to arrive and the latest to leave.

Hypopygiopsis fumipennis (Walker) (Fig. 13)

With 95 visits this was the third most frequent calliphorid on *R. zippelii* in S Thailand but was uncommon in W Malaysia. The species is newly recorded from Thailand. It can be slightly larger than *H. infumata* and, being just as variable in size, its pollinating potentiality is similar. But *H. fumipennis* infrequently attempted to enter the circumambulator and it appears to be an exceptional pollinator only. Male behaviour is as in *H. infumata*.

Hypopygiopsis tumrasvini Kurahashi

A very scarce species with only one sighting. Size and behaviour are as in *H. infumata*. It is more frequent in northern areas of S Thailand where a female acquired pollen of, and males exhibited rendezvous behaviour near, *Ra. kerrii* (BÄNZIGER, 1991 and in prep.).

Lucilia papuensis Macquart

Only one specimen was observed on *R. zippelii* at site (a) but a few were baited with

faeces and foul fish.

Carrion Fly Behaviour Near and on *R. zippelii*

Flower visitation may start as early as 0750 h with the first sporadic calliphorids, and end at dusk when the last ones leave. None were seen at night (4 vigils throughout the night at hourly intervals while watching flower opening in Thailand; none made in Malaysia). Increase in fly numbers was slow till mid-morning, when a faster pace set in to reach a maximum about 1200–1500 h. Flies often arrived in small groups rather than singly and, interestingly, often in mixed species groups. Sunflecks reaching the flower or its vicinity increased fly activity. Sometimes 5–6 flies were present at the same time on a flower (Fig. 1) and the maximum was 9. Visitation continued for many days, long after pollen was depleted.

Flies first settled on leaves, branches or other projecting objects in the close vicinity of the flower or landed directly on it, generally after some zig-zag flying over it. Landing was primarily on the furry hairs covering the lobes, especially the mid section. The caudate appendages were less frequently alighted upon, which is somewhat unexpected since according to KUGLER (1956) and VOGEL (1965) flies generally land on such tail-like processes emanating odour from osmophores (VOGEL, 1962). However, early morning settling when flowers were not yet fully opened, was more frequent on the appendages which were then most prominent. Direct settling onto the reddish ampulla was infrequent.

After a few seconds the fly extruded the labella to probe the substrate and started to crawl around as if in search of something. Crawling on the furry hairs often led to meeting the nectar pads (Fig. 10) after the fly pushed itself through or around the tuft hairs. Some individuals climbed onto the ampulla, probed there for a few moments and advanced further onto the furry hairs on the other lobe. If a fly landed on the caudate appendages, it generally crawled down towards the geniculate section, proximally to which it found the pads with the ramenta where it eagerly sucked nectar.

Female calliphorids have a penchant to explore cavities, probably because these are the preferred oviposition sites. Most individuals attempted to crawl down the wall of the inner tube towards the circumambulator. However, upon reaching the annular gap, average-sized pollinators were likely to back up again after a first encounter with it as the gap is slightly narrower than the height of their thorax (where flies are widest dorso-ventrally). To overcome the gap, which may require several attempts, the fly had to slightly squeeze itself through (Fig. 2). Since the fly and the anthers are not elastic, the furry tangle had to be pushed down. As the thorax negotiated the row of anthers a load of pollen mush (if present) was smeared onto the dorsum. Some individuals then backed up again—with or without a pollen load—but some penetrated further and reached the circumambulator. Small individuals penetrated unhindered, often without smearing off any mush but sometimes a large drop protruded sufficiently to be caught by the dorsum of the fly. Very large individuals, or average specimens of the large species of *Hypopygiopsis,* may not be able to push down sufficiently the tangle of furry hairs and retreated up the wall.

In the circumambulator the fly probed the substrate, then crawled for brief periods along the circumambulator (Fig. 3). Some pollinators circumambulated the column for

more than 360° but most left again after proceeding for less than a third to a half of the circular route. Crawling in the circumambulator did not necessarily entail pollen acquisition as the ceiling was higher than the fly's back. Flies could touch the ceiling when they lifted themselves on their legs, a curious behaviour which occurred often. Occasionally a fly made an about turn which also caused it to touch the ceiling. Moreover, the pollen mush did not necessarily collect at the lowest point of the ceiling but, due to capillary forces, it was sometimes drawn and smeared there by the pollinators themselves after their backs got smeared while negotiating the gap. Other flies could subsequently acquire pollen mush while circumambulating.

To leave the flower the fly climbed up and squeezed back through the gap (Fig. 5). This could result in acquiring new or additional pollen (Fig. 6), or in substituting already present pollen. The fly continued the climb and upon leaving the tube it flew off or crawled around on the furry tangle as when it first arrived. Some repeated the whole behaviour and re-entered the circumambulator.

I remarked no difference in fly behaviour between male and female *R. zippelii*. They rubbed their thorax back against the stigma instead of the anthers. Unfortunately, no calliphorids were seen with pollen on the only two fresh female flowers studied. In simulation experiments to verify pollen delivery, two dead *L. porphyrina* with a dry smear on the thorax were gently pushed through the gap, along the circumambulator and out again, which resulted in the reliquefaction of the pollen clot by, and its sweeping onto, the fluid–soaked stigmatic fascia.

'Mistake' Oviposition

While crawling on the lobe, some *L. porphyrina* performed curious 'repeated oviposition attempts' during which the ovipositor was extruded and wriggled into the tangle of furry hairs as when normally ovipositing, but no egg was laid. The fly constantly moved on and repeated the same behaviour which could continue for minutes. Evidently one of the many stimuli necessary for oviposition was missing.

Nevertheless, at least 14 specimens of *L. porphyrina* (Fig. 12) actually did lay up to 250 eggs each, mostly 100–200 (Tables 1–6). These were typically laid singly, or more rarely in small groups of 2–3, dispersed all over those parts of the flower which were covered by furry hairs and partly in the circumambulator. Five *C. pinguis* and two *C. villeneuvei* laid 20–200 eggs each but these were in one, or more rarely in two or three, dense clutches laid in the circumambulator (Figs. 11, 14). One *H. infumata* laid 4 eggs into the circumambulator.

Laying lasted 15–20 min during which time the flies were very unresponsive to outside influences. Sometimes two or three females laid at the same time, evidently due to pheromone action as shown in *L. cuprina* (Wiedemann) on sheep by BARTON BROWNE (1969). Eggs were laid on the first, second and/or the third flowering day of *R. zippelii*. Unexpectedly, no calliphorid eggs were laid on any of the 9 flowers at site (b) in either study year although *L. porphyrina* frequently exhibited 'repeated oviposition attempts'. At the other sites 9 flowers (8 males and 1 female) were each oviposited upon with a total of 2–1000 eggs, mostly 100–200 (Fig. 16). On a further 9 flowers (8 males and 1 female) at sites (a) and (c) no calliphorid eggs were found. While this might mean that, overall,

at these sites 50% of the flowers were oviposited upon, in reality this finding is not conclusive. In fact, observations of some of these latter 9 flowers had been possible only during the first and second flowering day, hence subsequent oviposition cannot be excluded. The remaining flowers were found when already 2–3 days old, which does not exclude the possibility that, before I found them, ants might have preyed upon the eggs; *Pheidole* sp. have repeatedly been observed abducting eggs (Fig. 15).

Except for larval *L. sericata* (Meigen), which have been reported to be able to breed in decaying plant matter (GREEN, 1951), the development of larval *Lucilia* and *Chrysomya* species associated with *R. zippelii* is dependent on decaying animal remains. Therefore, the carrion flies' progeny on *R. zippelii* are doomed to starvation or predation by ants. Surviving non–predated eggs hatched the day following deposition and the young larvae restlessly crawled around the flower till exhaustion for about a day, dying or leaving the flower for the ground. None was seen to eat and grow, even on older flowers starting to decompose. As a further check, two flowers were cut and kept enclosed in jars to see if any larvae developed: none did. However, larvae of other dipterous species, most likely Drosophilidae which are known to breed in decaying vegetable matter, appeared to prosper.

Non-pollinators

Full dupes

These visitors are deceptively attracted by the various lures without obtaining any substance of known use to them. It must be assumed that they are misled by fake odours released by the flower in imitation of carrion, excrement or other decomposing animal matter on which they or their progeny feed.

Micropezidae (Diptera)
Mimegralla cedens ssp. *thaiensis* Cresson. A few specimens settled on the caudate extensions. They were probably misled by the extensions' odour since they were often seen to settle on excrement.

Platystomatidae (Diptera)
Scholastes cinctus (Guérin-Méneville) (Fig. 22) and *Euthyplatystoma rigida* (Walker). Three and one specimens, respectively, landed on the lobes at site (b). They barely walked but probed the tangle of furry hairs and then left. Many more specimens of these species fed from faeces at sites (b) and (c), while and additional, unidentified relative did so also at site (a). No nectar was sucked. Adults are known to feed from decomposing organic matter, especially faeces, as do their larvae.

Stratiomyidae (Diptera)
Ptecticus melanura (Walker). One specimen settled on the flower. No nectar was sucked. The species was also seen flying around *Ra. kerrii* and *Sapria* cf. *poilanei* Gagnepain (BÄNZIGER, unpubl.). According to Rozkošný *(in litt.)* and ROZKOŠNÝ & KOVAC (1994), the larval feeding habits of *P. melanura* are not known but larvae of other species of the genus are phytosaprophages with some tendency to coprophagy.

Figure 1. Seven carrion flies (females in all illustrations unless otherwise stated) on *R. zippelii: C. megacephala* (upper arrow), male *L. porphyrina* (lower arrow) among several *C. pinguis* or *C. chani.* A yellow *Trigona* bee is hovering above a nectar pad (upper left corner).

Figure 2. *H. infumata* intruding into the circumambulator of *R. zippelii.*

Figure 3. *Chrysomya* sp. circumambulating the column.

Figure 4. Same *H. infumata* of Fig. 2 climbs and leaves the tube with a pollen smear.

Figure 5. *C. pinguis* or *C. chani* in the act of smearing off pollen mush while negotiating the annular gap between anthers and furry hairs.

Figure 6. An instant later, the same specimen with an exceptionally large pollen smear.

Figure 7. *L. porphyrina* climbing the tube with a freshly acquired pollen smear.

Figure 8. *C. villeneuvei* with a pollen smear.

Figure 9. Two *C. pinguis*, each with an old, clotted pollen mush smear.

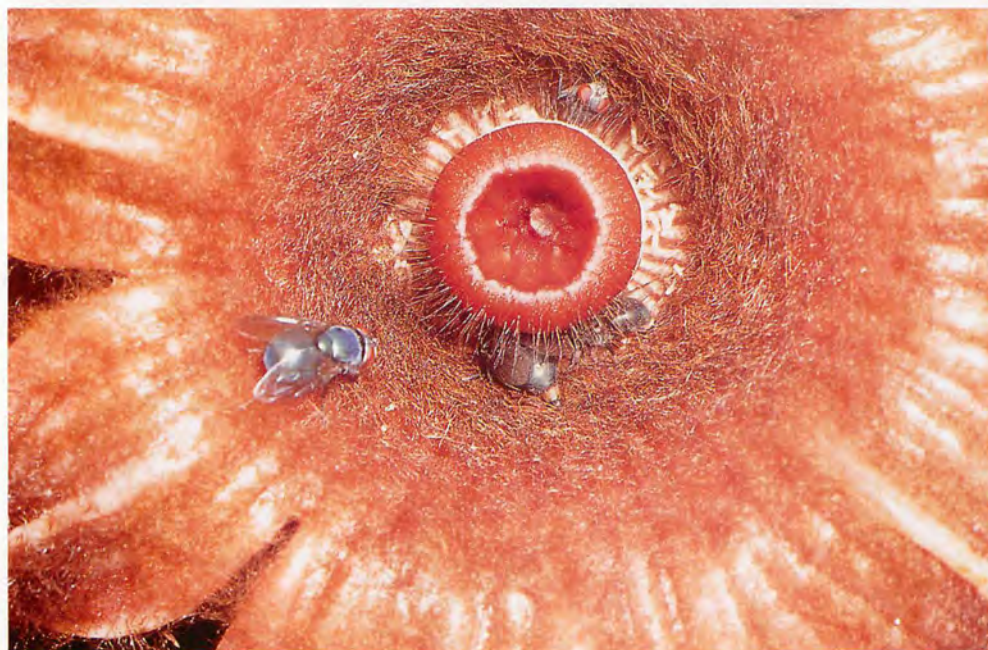Figure 10. *L. porphyrina* sucking nectar. Note the labellum on the wet nectar pad.

Figure 11. Three *C. pinguis* ovipositing in the circumambulator. Note the extended ovipositors and the eggs. One *L. porphyrina* is on the perigone.

Figure 12. Two *L. porphyrina* ovipositing on the perigone of *R. zippelii*. Note the extruded ovipositors and the yellowish eggs.
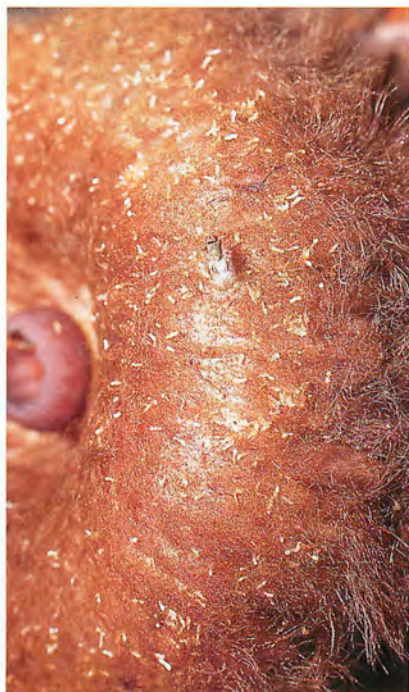
Figure 13. Hundreds of eggs of *L. porphyrina* laid between and below the furry hairs.

Figure 14. *Pheidole* sp. ants abducting a clutch of eggs of *C. villeneuvei*.

Figure 15. A clutch of eggs of *C. villeneuvei* laid in the circumambulator.

Figure 16. Male *H. fumipennis* lurking for females in the vicinity of *R. zippelii*.

Figure 17–22. Non-pollinating visitors of *R. zippelii*. Parasitic *Lophomyrmex* ants bite off nectariferous tissue and hairs (17). Opportunists *Meranoplus* ants (18) and honey bee *(Apis cerana)* (19), half dupes *Atherigona* fly (20) and *Polybioides* wasp (21) suck nectar without causing damage. Full dupe *Scholastes cinctus* finds no reward on *R. zippelii* (22).

Staphylinidae (Coleoptera)
A small unidentified staphylinid beetle entered and crawled around in the circumambulator; it is far too small to touch the anthers. Many staphylinids are necrophagous.

Half dupes

As far as can be established, these visitors are half–deceptively attracted because, while being misled by fake oviposition or feeding sites, they obtain nectar which is part of their natural diet. Nectar can evidently be perceived from some distance, at least by bees.

Sarcophagidae (Diptera)
Sarcophaga sp. near *peregrina* (Robineau-Desvoidy) and other spp. Although 8 flesh flies settled on *R. zippelii* at the three sites, none exhibited a behaviour which might have lead to pollen acquisition. None entered the circumambulator or larviposited. One settled on the caudal appendages. Some sucked nectar.

Muscidae (Diptera)
Neomyia claripennis (Malloch). Three specimens visited the flower, 2 settled on the lobes and sucked nectar, one landed on the ampulla, none approached the circumambulator. This species is superficially very similar to blow flies with their metallic blue shine. Adults were strongly attracted to faeces though they also visited foul fish.
Atherigona, two different species close to *lamellifera* Pont & Magpayo. These small flies frequently settled on the caudal appendages and crawled to the nectar pads where they sucked nectar (Fig. 20).

Unidentified families of Diptera
Various mosquitoes occasionally landed on and probed the furry hairs, possibly deceived by odours (CO_2 emanation?), vision and/or tact.

Vespidae (Hymenoptera)
Polybioides sp. probably *gracilis* v.d. Vecht (Fig. 21) were occasionally flying around the flower at sites (a) and (b). Some landed on the lobe tip to suck nectar. They were also present on nectarless *Ra. kerrii* while some specimens bit off flesh from the head of a macaque carcass (BÄNZIGER, 1991) indicating that *Polybioides* is probably attracted, at least in part, to carrion.

Opportunists

These cheat the flower. Without performing any pollination act they steal nectar, part of their natural diet, but do not harm the flower which continues to be visited by pollinators. It must also be pointed out that nectar in *R. zippelii* is not directly involved in the pollination and therefore function more like extrafloral nectaries (BÄNZIGER, 1995).

Apidae (Hymenoptera)

Apis cerana F. (Fig. 19). Well over 30 Asian honey bees sucked nectar. They always landed at the nectar pads and rarely explored other flower areas. This indicates that, at least at close range, they were attracted by a nectar clue.

Trigona iridipennis Smith and *T. melina* Gribodo (Fig. 1). Many Meliponinae (stingless bees) frequently sucked nectar but occasionally one ventured down the tube but no pollen was taken or smeared off as they are too small for the back to touch the anthers. On many occasions they also took sweat from the author's skin. In the Neotropics they exhibit strong necro—and coprophagy, often competing successfully against carrion flies (e.g. BAUMGARTNER & ROUBIK, 1989) though, so far, I have seen no aggressive behaviour against calliphorids on *R. zippelii* nor necrophagy among SE Asian species.

Formicidae (Hymenoptera)

Paratrechina sp., *Meranoplus* sp. (Fig. 18) and *Technomyrmex* sp. Ants belonging to these genera fed on nectar from the nectariferous pads at site (a), and the latter two at sites (b) and (c). The ants were nectar thieves which did not harm the nectaries by biting off tissue as the parasitic ant did (see below). Ants of the three genera are known to take nectar from various flowers; as trophobionts they also imbibe honeydew excreted by various Homoptera or other sweet exudates of other insects.

Gnamptogenys sp. Ants of this genus are both predators as well as trophobionts. They took nectar without biting off nectar tissue at site (b).

Camponotus probably *gigas* (Latreille). A very large ant which took nectar at site (b).

Pheidole sp. (Fig. 15). These ants were predators of the eggs carrion flies laid on *R. zippelii*. These ants are food generalists taking whatever they can grab.

Odontoponera transversa F. Smith. The ant attacked and killed a stingless bee (*Trigona* sp.) which was sucking nectar. Ants of this genus do not take nectar but are predators. It is not clear whether they used the flower as a hunting ground or whether the kill was purely accidental.

Nymphalidae (Lepidoptera)

Three individuals of *Euthalia pardalis* visited the nectar pads to feed.

Satyridae (Lepidoptera)

An unidentified species sucked nectar.

'Parasites'

These actually damage the flower by biting off nectariferous tissue, ramenta, furry hairs or other tissues. The term 'parasite' is used here in a broad sense (e.g. DÖNGES, 1980) which includes organisms harming their host by living on it for a relatively brief period only (so—called temporary parasites).

Formicidae (Hymenoptera)

Lophomyrmex sp. (Fig. 17). This ant is an intense nectar feeder which also bites off the nectariferous tissue. It can be very destructive when numerous and can completely

obliterate all the nectaries in a couple of hours. Occasionally they also bite off hairs as well as soft tissues though the hard parts are left and remain as black flower skeletons for months.

Gryllacrididae (Orthoptera)

Gryllacris sp. A nocturnally active species which ate parts of the nectaries and other sections of soft tissue of the flower. A specimen gnawed at *Sa.* cf. *poilanei* (in prep.).

DISCUSSION

The most comprehensive faunistic survey of Calliphoridae in Thailand (TUMRASVIN ET AL., 1979) has listed 42 species in 15 genera. *Chrysomya, Lucilia, Hypopygiopsis* and *Hemipyrellia,* the genera involved in the pollination of *R. zippelii,* were represented by 16 species in that survey. In my study a surprisingly high proportion, 9 of the 16 species mentioned (besides the one newly recorded from Thailand), were found to be associated with *R. zippelii* at the site in S Thailand. At the Malaysian sites 7 species were encountered. The faunal composition has some bearing for the understanding of the pollination syndrome.

The most frequent pollinators of *R. zippelii,* viz. *L. porphyrina* and *C. pinguis,* breed in animal carcasses and since the flower induces 'mistake' oviposition and very low male presence, it can be assumed that *R. zippelii* mainly mimics carrion in a pollination syndrome based on brood-site deception. Carrion imitation is not evident at first sight in *R. zippelii* because the flower's aspect, and the absence of a cadaveric stench, do not remind one of a carcass. No doubt *R. zippelii*'s attraction is broad and includes additional lures. One is an excrement/cheesy odour faking food sources for adult calliphorids as well as a breeding site for such species as *C. megacephala,* the Oriental latrine fly, a well-known synanthropic species capable of breeding also in faeces (*e.g.* in Malaysia, SULAIMAN ET AL., 1989). The full dupes, and to a lesser degree the half dupes, mentioned are evidently also deceptively attracted by this lure. Further, a certain degree of attraction by mimicking orifices and wounds of live mammals cannot be excluded despite the noteworthy lack of visits by calliphorids causing myiasis (infestation of live vertebrates with dipterous larvae). The absence of one such species, *C. bezziana* Villeneuve, known as the Old World screw-worm fly, is almost certainly due to its very low population density (SPRADBERY, 1979; Wyatt, pers. comm.), not necessarily because the flower lacks appropriate lure for this obligatory parasite of ungulates where it devours live tissue. This interpretation is reinforced by the concomitant lack on *R. zippelii* of two further noteworthy blow flies. One, *L. cuprina,* is both a myiasis-causing and a carrion-breeding fly and therefore ought to be expected on *R. zippelii* even if the flower only fakes carrion, was it not that the fly is likewise scarce (GILMOUR ET AL., 1946). Absence of the second, *C. rufifacies* (Macquart), primarily a carrion breeder which can also be involved in myiasis, appears to be due to its preference for a different habitat from that of *R. zippelii.* It is an important pollinator of *Ra. kerrii* in the seasonally drier regions of southern Thailand north of the Isthmus of Kra, but was missing on this rafflesia in more humid areas south of Kra and also lacking on *Ra. cantleyi* Solms-Laubach at the study sites of *R. zippelii* in yet more humid W Malaysia (BÄNZIGER, 1991 and unpubl.). According to BAUMGARTNER (1993) *C. rufifacies* makes up only 9%

of total blow fly catches at baits in SE Asia but is dominant in drier areas in Australia.

   C. megacephala's scarcity on *R. zippelii* can be explained by its preference for more open habitats or by its synanthropy; I found it common around human habitation in Chiang Mai as well as around Orang Asli settlements just outside dense forest but scarce on *R. zippelii* within the same forest. The scarcity of *L. papuensis* conforms to observations made on *Ra. kerrii* where it was only occasionally seen (BÄNZIGER, unpubl.). Together with *C. pinguis* it is one of the pollinators of *Ra. pricei* Meijer in Sabah (N Borneo) (BEAMAN ET AL., 1988) but the relative frequency of the two flies was not studied. It is a little–known species like *C. villeneuvei* and *C. chani,* both also pollinators of *Ra. kerrii* (BÄNZIGER, 1991 and unpubl.). *C. chani* was the most common pollinator of *Ra. cantleyi,* followed by *C. villeneuvei,* while *C. pinguis* was strangely missing altogether on this rafflesia despite the fly's higher frequency in the same habitat (preliminary findings needing more field observations).

   The scarcity of *He. ligurriens* at Thai sites and absence at the Malaysian sites may be due to a more northerly distribution of the species: it is not listed in SULAIMAN ET AL. (1989) and was among the four most common calliphorids in the Hong Kong area (SO & DUDGEON, 1990). Little is known about the three *Hypopygiopsis* species but they are found mainly in southern regions of Thailand and in Malaysia, *H. fumipennis* being recorded for the first time in Thailand.

   L. porphyrina and *C. pinguis* are common and widely distributed in forest habitats and their dominance in the pollination of *R. zippelii* is not surprising. *C. pinguis* is also a pollinator of *Ra. pricei* (BEAMAN ET AL., 1988) and both species pollinate *Ra. kerrii.* Furthermore, a female *L. porphyrina* with a dry pollen smear of *Sapria himalayana* Griff. (acquisition not witnessed but positioning and colour of the smear, as well as microscopic examination of the pollen grains, confirmed it to be of this flower) was recently observed to enter a female *Sa. himalayana* in N Thailand. Unfortunately, this fly did not crawl down below the disk as the species often does. It flew off but the same individual (recognizable by the particularly shaped pollen smear) was caught two hours later near another cluster of *Sa. himalayana* 200 meters away (BÄNZIGER, in prep.).

   Among non-pollinating visitors of *R. zippelii* the Sarcophagidae hold an intriguing position *vis-à-vis* the Calliphoridae and the Rafflesiaceae. *Sarcophaga* spp., whose adult and larval feeding habits are similar to those of carrion flies, sometimes landed on, and very occasionally entered the tube of, *R. zippelii, Ra. kerrii* and *Ra. cantleyi,* but they never ventured into the circumambulator or below the disk where they might have effected pollination. On the other hand, at least two species of *Sarcophaga* were found to be regular pollinators of *Sapria* sp. cf. *poilanei* which was scarcely visited by carrion flies (loc. cit.).

   Whereas some plants offer brood food for the progeny of their specific pollinators which oviposited on the plants (e.g. ARMSTRONG & IRVINE, 1990; HIME & COSTA, 1990; FEIL, 1992), a number of plants act by brood–site deception. 'Mistake' oviposition has not been noted in recent pollination studies of *Rafflesia* and *Sapria* spp. (BEAMAN ET AL., 1988; BÄNZIGER, 1991 and in prep.) but it is known to occur in *Aristolochia* spp. (CAMMERLOHER, 1923), stapelias (Asclepiadaceae) (FAEGRI & PIJL, 1979), and in the slipper orchids *Paphiopedilum rothschildianum* (Reichb. f.) Stein and *P. callosum* (Reichb. f.) Stein though significantly not in *P. villosum* (Lindl.) Stein (ATWOOD, 1985; BÄNZIGER,

1996 and in prep.). *R. zippelii*'s sabotage of the complex set of stimuli which guide oviposition in blow flies, causing them to waste hundreds of eggs, is remarkable. MERRITT & RICE (1984) have demonstrated the presence of tactile, olfactory and gustatory receptors on the ovipositor of *L. cuprina* which is able to monitor texture, odours, salts, pH and blood components (RICE, 1976, 1977). BARTON BROWNE (1979) mentioned in his review that this fly lays in cavities in the sheep fleece, which are places of high humidity and low light intensity, and that indole vapours and carbon dioxide are oviposition stimulants. It is very probable that *R. zippelii*'s furry hairs fake the texture of mammalian pelage while the circumambulator is a *de facto* cavity. Carbon dioxide release can be expected to be more in evidence in a non-photosynthetizing parasite. *R. zippelii*'s perplexing odours are likely to be a 'cocktail' of various volatiles (including indol) which may mimic the compounds released by carrion, wounds or infected orifices.

DETHIER ET AL. (1960) also mentioned that certain chemicals in sheep fleece may not induce oviposition but act as arrestants to keep the flies on the host. It is not clear whether *R. zippelii* produces a corresponding arrestant but, in a way, the flower's nectar, while being a real reward, functions similarly. It keeps the pollinators on the flower. It also induces them to crawl around in search for more, increasing their chances of entering the circumambulator. And, since the flies have a certain learning capacity (KUGLER, 1951), it promotes re-visitation of *R. zippelii*, important for pollen delivery onto a female. It should be noted that, whereas pure nectar is said to be odourless (KUGLER, 1970), the nectar of *R. zippelii* evidently possesses a clear attractancy of its own and is not just accidentally found by visitors enticed by decomposition smells, at least in the case of nectar–steeling Hymenoptera and Lepidoptera. *Apis cerana* and stingless bees may feed on filth (e.g. BAUMGARTNER & ROUBIK, 1989; pers. obs.), and many Lepidoptera take various mammalian body fluids (e.g. BÄNZIGER, 1985), but their behavioural pattern near and on *R. zippelii* leaves little doubt that they are directly attracted to the nectaries. Calliphorids also naturally visit flowers to suck nectar; without carbohydrates they cannot survive more than 2–3 days (BRODY, 1939). Thus *R. zippelii* is not fully deceptive and may be designated as a semi- or partially-deceptive flower *sensu* DAUMANN (1971).

With the finding of the unusual properties of the pollen of *Rhizanthes, Sapria* and *Rafflesia* (viz. clotting and hardening of the pollen mush, its retention of germinability in this state for an extended period and its reliquefaction on the fluid soaked stigma) it is clear that female flowers can be pollinated weeks after the pollen was acquired from a male. Observed cases of re-visitation by carrion flies with old pollen mush—mostly aged one to several days—numbered 18 and was as high as 38% of total pollen acquisitions in *L. porphyrina.* The vectors are strong fliers and thus capable of long distance pollination during their life span—in captivity up to 3 months, average 7 weeks (SALT, 1932; MACKERRAS, 1933). The New World screwworm fly *Cochlyomyia hominivorax* (Coquerel) has been proved to cover a maximum of 250 km in less than two weeks (HIGHTOWER ET AL., 1965) though more commonly some 50 km per week (HALL, 1991). *C. rufifacies* has been trapped at 6 km within 24 h after release (NORRIS, 1959). However, it is assumed that most specimens remain within a radius of a few km. Long distance pollination is generally connected with traplining where regular pollinators visit widely spaced flowers along certain routes which can be several km long (JANZEN, 1971, 1974). In calliphorids traplining is improbable. Unlike most flowering plants, carrion as a source of food is

highly unpredictable in time and space and calliphorids are unlikely to follow particular routes when in search for brood-sites. It should also be mentioned that *Co. hominivorax* can be attracted up to at least 150 m distance by the attractant swormlure-2 (BROCE ET AL., 1979) which appears to mimick the odour of its nutritional flowers (BROCE, 1980) .while it also contains volatiles emitted by decaying meat.

Because of *R. zippelii*'s ability to mislead pollinators to commit 'infanticidal' oviposition, the flower is a more efficient trickster than its close relatives *Sapria* and *Rafflesia* and hence it may appear to be a more advanced deceptive flower than the latter two (reasons for my reverting to the original view that *Rafflesia* is deceptive is mentioned in BÄNZIGER (1995)). However, besides the fact that *R. zippelii*'s nefarious effect on the pollinators' progeny reduces prospective pollinator populations—which suggests a less well adapted pollination syndrome—there are also several morphological and ecological features which additionally point to a more recent evolution in *Rhizanthes* than in its relatives. For instance, it appears less reduced morphologically: it retains nectaries (none present in *Sapria* and *Rafflesia*); the flower is relatively shallow and open with the reproductive organs quite readily accessible to pollinators compared to the deep kettle-traps with concealed reproductive parts of *Sapria* and especially *Rafflesia;* the number of lobes and the hairiness are less reduced, with 16 versus 10 and 5 lobes, respectively. In *Rhizanthes* speciation has barely started with at most two not clearly separable species, or more probably only one rather variable species (MEIJER & VELDKAMP, 1988; BÄNZIGER, 1995) against at least 2 in *Sapria* (HANSEN, 1973) and some 14–15 in *Rafflesia* (MEIJER, 1984; MAT-SALLEH & LATIFF, 1989). *Rhizanthes* has a wider host range: 2 families with 6 spp. (PIJL, 1933; MEIJER & VELDKAMP, 1988; BÄNZIGER, 1995) though studies focussing on host relationship may reduce this. This compares with 1 family with 3 species each for *Sa. himalayana* (ELLIOTT, 1990) and *Sa. poilanei* (GAGNEPAIN, 1941). *Rafflesia*'s host spectrum has recently been narrowed down significantly (LATIFF & MAT-SALLEH, 1991; LATIFF, pers. comm.; BÄNZIGER, 1991, 1995), with several species parasitizing the same host species, and very few confirmed additional hosts possibly restricted to fringe areas. Finally, the insect fauna associated with flowering *R. zippelii* is much broader with at least 6 pollinator and 4 exceptional/potential pollinator species, 5 full dupes, 6 half dupes, 12 opportunists and 2 'parasites', i.e. a total of 35 species of 12 families in 5 orders. In *Sapria* pollination studies are still in progress but it is clear that these flowers are more selective, as are *Rafflesia*. *Ra. kerrii,* in a similar habitat as *R. zippelii,* had 4 pollinators, 2 exceptional pollinators and some 8 full dupes—only 14 spp. of 7 families in 3 orders (pers. obs.).

CONCLUSION: THE POLLINATION PROCESS

From results obtained so far the pollination sequence of *R. zippelii* is:

1.   Probably from a distance of many dozens of metres a female carrion fly is alerted and attracted to a flower by its odours ('stuffy room' with a weaker excrement-like odour).

2.   At close distance the fly is possibly additionally guided by sight—a hairy, rufous body centered by the reddish ampulla, the whole probably mimicking mammalian carrion and possibly orifices or wounds. Nectar may also be advertised.

3.   After landing on a lobe, or more rarely on a caudate appendage, the fly crawls

around probing the furry tangle with its labella. It generally stops to suck at the nectaries (Fig. 10). Some may oviposit (Figs. 11, 12), presumably misled by the flower's odours and furry hairs.

4. Since carrion flies tend to enter cavities for egg laying, the fly is likely to attempt intrusion into the circumambulator by crawling down the furry tube wall (Fig. 2). Here it has to negotiate the annular gap formed ventrally by the furry tangle (which must be pressed down to pass) and dorsally by the row of anthers (if the flower is a male) from where a load of pollen mush is smeared onto its dorsum.

5. The pollinator may start circumambulating around the column (Fig. 3), occasionally reversing direction, an about-turn sometimes leading to pollen acquisition. This also occurs when the pollinator lifts itself somewhat on its legs and the dorsum touches a drop of pollen mush.

6. The pollinator leaves by crawling up the tube wall, pollen often being acquired while passing the gap (Fig. 5).

7. The pollinator may fly away or fly back or continue to crawl on the flower and may repeat the whole or part of the sequence 3–6.

8. Pollen delivery onto a female flower is analogous. Pollen mush is swept onto the stigmatic fascia (same location as the ring of anthers) when the pollinator negotiates the gap. Delivery may occur on a nearby female flower shortly after acquisition, or up to weeks later in a flower potentially dozens of km away when dried pollen mush is quickly reliquefied and 'sponged' off by the papillae of the fluid soaked stigma.

ACKNOWLEDGMENTS

Table 1. Behavioural patterns of blow flies *L. porphyrina* (Lp), *C. pinguis* + *C. chani* together (CpCn) and *C. villeneuvei* (Cv) on 4 male *R. zippelii* at site (a), Thailand. Females only unless otherwise stated.

flower code	male 11.1			male 5.8		males 5.1 + 5.2
flower opening date	6.4.95			15.4.95		18.4.95
watching date	6.4.95	7.4.95	8.4.95	15.4.95	16.4.95	18.4.95
watching time	0700–1630 h	1030–1600 h	1100–1530 h	0700–1630 h	1000–1600 h	0715–1315 h
blow fly species	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv
landed on flower	26/15/9	28/10/1	24/15/2	11/24/2	2/4/2	12/16/4
carrying pollen — mushy	3/0/0	0/0/0	0/0/0	0/0/0	0/0/0	1/0/0
solid	2/0/2	5/0/1	2/0/0	0/0/0	0/0/1	0/0/0
on arrival — undet.[1]	1/0/0	0/0/0	0/0/0	0/0/0	0/0/0	2/0/0
crawled into tube	11/11/3	8/2/1	(6/7/0)[4]	2/10/5	0/0/1	3/10/2
entered circumambulator	7/7/3	3/2/0	(0/0/0)[4]	2/10/5	0/0/1	3/10/2
acquired pollen	4/11[2]/0	/[5]	/[5]	0/1/0	/[5]	(3/4/0)[3]
oviposited	0/0/0	>200 eggs by several Lp	~800 eggs by 5 Lp	0/0/0	~20 eggs by Cv	>130 eggs on 5.2 by Lp
males on flower	0/0/0	0/0/0	0/0/0	0/4/4	0/1/1	0/1/0

Table 2. Behavioural patterns of blow flies *C. megacephala* (Cm), *H. fumipennis* (Hf), *H. infumata* (Hi) and *He. ligurriens* (Hl) on 4 male *R. zippelii* at site (a), Thailand. Females only unless otherwise stated.

flower code	male 11.1			male 5.8		males 5.1 + 5.2
flower opening date	6.4.95			15.4.95		18.4.95
watching date	6.4.95	7.4.95	8.4.95	15.4.95	16.4.95	18.4.95
watching time	0700–1630 h	1030–1600 h	1100–1530 h	0700–1630 h	1000–1600 h	0715–1315 h
blow fly species	Cm/Hf/Hi/Hl	Cm/Hf/Hi/Hl	Cm/Hf/Hi/Hl	Cm/Hf/Hi/Hl	Cm/Hf/Hi/Hl	Cm/Hf/Hi/Hl
landed on flower	0/22/6/0	0/17/6/0	0/6/2/0	2/6/9/1	0/8/8/0	0/1/6/1
carrying pollen on arrival	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0
crawled into tube	0/7/0/0	0/1/0/0	0/0/1/0	2/1/6/1	0/0/0/0	0/1/1/1
entered circumambulator	0/0/0/0	0/0/0/0	0/0/0/0	2/0/1/2[1]	0/0/0/0	0/0/0/1
acquired pollen	0/0/0/0	/[2]	/[2]	2/0/0/0	/[2]	0/0/0/1
oviposited	0/0/0/0	0/0/0/0	0/0/0/0	4 eggs by Hi	0/0/0/0	0/0/0/0
males on flower	0/0/0/0	0/0/0/0	0/0/0/0	1/0/0/0	0/0/0/0	0/0/0/0

Remarks: 7 male *H. fumipennis* lurked for females in the vicinity; one grabbed a female in flight and flew off in copula. [1]Pertains to one individual which entered twice. [2]Pollen depleted already in the afternoon of opening day. A female *H. tumrasvini* was caught near *R. zippelii*.

Table 3. Behavioural patterns of blow flies *L. porphyrina* (Lp), *C. pinguis* + *C. chani* together (CpCn) and *C. villeneuvei* (Cv) on a female *R. zippelii* at site (a), Thailand. Females only unless otherwise stated.

flower code	female 9.1				
opening date	9.4.95				
watching date	9.4.95	10.4.95	11.4.95	12.4.95	13.4.95
watching time	0700–1700 h	0930–1800 h	1000–1700 h	1100–1500 h	1130–1530 h
blow fly species	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv
landed on flower	18/27/0	13/13/0	10/13/0	0/0/0	0/0/0
carrying pollen on arrival	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0
crawled into tube	1/10/0	2/4/0	1/2/0	0/0/0	0/0/0
entered circumambulator	0/9/0	2/3/0	0/1/0	0/0/0	0/0/0
delivered pollen onto stigma	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0
oviposited	~200 eggs by 4 Cp	0/0/0	0/0/0	0/0/0	0/0/0
males on flower	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0

Table 4. Behavioural patterns of blow flies *C. megacephala* (Cm), *H. fumipennis* (Hf), *H. infumata* (Hi) and *He. ligurriens* (HI) on female *R. zippelii* at site (a), Thailand, 1995. Females only unless otherwise stated.

flower code	female 9.1				
opening date	9.4.95				
watching date	9.4.95	10.4.95	11.4.95	12.4.95	13.4.95
watching time	0700–1700 h	0930–1800 h	1000–1700 h	1100–1500 h	1130–1530 h
blow fly species	Cm/Hf/Hi/HI	Cm/Hf/Hi/HI	Cm/Hf/Hi/HI	Cm/Hf/Hi/HI	Cm/Hf/Hi/HI
landed on flower	0/8/7/1	0/3/8/1	0/10/1/2	0/0/0/0	0/0/0/0
carrying pollen on arrival	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0
crawled into tube	0/1/1/1	0/2/5/1	0/5/0/2	0/0/0/0	0/0/0/0
entered circumambulator	0/0/1/1	0/0/0/1	0/0/0/2	0/0/0/0	0/0/0/0
delivered pollen onto stigma	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0
oviposited	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0	0/0/0/0
males on flower	0/0/0/0	0/0/0/0	0/0/1/0	0/0/0/0	0/0/0/0

Remarks: 2 male *H. fumipennis* and 8 male *H. infumata* lurked for females in the vicinity. 2 *H. infumata* grabbed a flying female each, one flying off in copula; a third mistakenly grabbed a *H. fumipennis* female which was released later.

Table 5. Behavioural patterns of blow flies *L. porphyrina* (Lp), *C. pinguis* + *C. chani* together (CpCn) on one female and 4 male *R. zippelii* at site (b), Malaysia, 1994 and 1995. Females only unless otherwise stated.

flower code	0.3 female		0.4 male		0.5 male		0.6 male		1.1 male
flower opening date	22. or 23.1.94		28.1.94		29.1.94		1.2.94		25.1.95
watching date	24.1.94	25.1.94	28.1.94	29.1.94	30.1.94	31.1.94	1.2.94	2.2.94	25.1.95
watching time	1440–1615 h	1000–1630 h	0930–1920 h	0930–1730 h	0950–1800 h	1230–1640 h	1500–1830 h	1030–1300 h	1000–1030 h
blow fly species	Lp/CpCn	Lp/CpCn	Lp/CpCn	Lp/CpCn	Lp/CpCn	Lp/CpCn	Lp/CpCn	Lp/CpCn	Lp/CpCn
landed on flower	7/8	5/4	50/33	20/13	25/30	20/13	10/9	18/4	3/0
carrying pollen on arrival	0/0	0/0	0/0	0/0	0/4	0/1	0/0	1/1	0/0
crawled into tube	7/8	1/1	17/17	9/11	11/18	5/9	5/8	5/1	0/0
entered circumambulator	6/7	1/1	15/17	7/9	10/16	5/9	5/7	4/1	0/0
acquired pollen	-----	-----	1/4	6/6	2/10	0/2	5/6	0/0[1]	0/0
oviposited	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
males on flower	0/0	0/0	0/0	1/0	2/0	0/0	0/0	0/0	0/0

Remarks: 3 *H. infumata,* 9 *H. fumipennis,* all females, on flower, nectar pads and half way down tube; one of latter attempted entering circumambulator, on 28. and 29.1.94. One male *H. fumipennis* lurked for females near flower. [1]Pollen already depleted on previous day.

Table 6. Behavioural patterns of blow flies *L. porphyrina* (Lp), *C. pinguis* + *C. chani* together (CpCn), and *C. villeneuvei* (Cv) on 7 male *R. zippelii* at site (c), Malaysia, 1995. Females unless otherwise stated.

flower code	male 2.1.0		male 2.5.1		males 2.5.2+2.5.27+2.5.28			males 2.5.26+2.4
flower opening date	16.1.95		20.1.95			27.1.95		31.1.95
watching date	16.1.95	17.1.95	20.1.95	21.1.95	27.1.95	28.1.95	29.1.95	31.1.95
watching time	1030–1730 h	1130–1600 h	1245–1745 h	1400–1500 h	1315–1500 h	1300–1730 h	1330–1500 h	1030–1645 h
blow fly species	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv	Lp/CpCn/Cv
landed on flower	21/19/9	2/4/5	12/9/5	2/1/1	(20/10/0)³	(5/3/1)³	0/0/0	47/19/2
carrying pollen ┐ mushy	1/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	2/0/0
solid	0/1/0	0/0/0	1/0/0	0/0/0	0/0/0	0/0/0	0/0/0	2/1/0
on arrival ┘ undet.¹	5/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	4/0/0
crawled into tube	11/2/2	0/0/1	5/7/5	0/0/0	(10/5/0)³	(2/1/1)³	0/0/0	20/10/0
entered circumambulator	10/2/2	0/0/1	4/7/4	0/0/0	0/0/0	0/0/1	0/0/0	13/6/0
acquired pollen	11²/3/2	?⁴	4/5/4	?⁴	0/0/0	?⁴	?⁴	11/9²/0
oviposited	21 eggs by Lp	17 eggs by Lp	2 eggs by Lp	0/0/0	>250 eggs by Lp on 2.5.27	Lp, Cp, Cv each>100 eggs on 2.5.2.	0/0/0	0/0/0
males on flower	3/5/0	0/0/0	0/3/0	0/0/0	0/0/0	0/0/0	0/0/0	0/8/0

Remarks: ¹Undeterminate. ²Some pollen acquired during unsuccessful attempts to enter circumambulator. ³Estimate. ⁴Pollen depleted already by afternoon of opening day. On 16. and 20.1.95 4 male and 2 female *C. megacephala*, 5 female *H. fumipennis* and 1 male *H. infumata* were seen on flower.

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Appendix 1: additional notes

During a new visit to site (a) 30.3–9.4.96 following additional data on *R. zippelii* were obtained.

Five additional clusters were found, all on aerial roots of *T. pedunculare* except one which had old scars on the stem. Three clusters which in the previous year appeared to have no extant live *R. zippelii* showed no sign of recovery. Several clusters which flowered abundantly last year had few flowers/buds or were sterile this year, while only a few clusters had more flowers than last year. Apparently two flowers had been fertilized and were now producing fruit.

Additional morphometric data of two females (1 flower/1bud) (in cm): length of caudal appendages 2.5–3.8/2.2–3.2; width of perigone lobes 1.4–2.0/-; column height 1.9/1.8; width of stalk of column 0.95/0.95; ampulla height 0.6–0.7/0.55; external diameter of ampulla at maximum width 1.7/1.5; diameter of ampulla crest 1.1/0.85 x 0.95; crater depth 0.95/0.8; width of stigmatic fascia 0.8/0.8; width of neck 3.4/3.3; diameter of flower (without appendages) 15/circumference of bud 17.7.

The stigma of the only freshly opened female flower seen was wet on the first two days but in the afternoon of the second it showed signs of drying (in *Rafflesia* and *Sapria* spp. I studied the stigma was wet for at least 5–6 days). None of the many visiting flies (usual spp.) carried fresh pollen mush; thorough check of the study area showed that no male flowered concomitantly with, or during the preceeding two weeks of, this female. However, in the afternoon of the second day, one *C. pinguis* with a dry pollen clot (presumably more than two weeks old) entered the circumambulator. The clot was not smeared off onto the stigma because at the entering point it was already somewhat dry and damaged by *Lophomyrmex* ants. A large *H. infumata* acquired a pollen smear from a male flower with an unusually wide gap between anthers and furry hairs (Fig. 2, 4). One *C. pinguis* fully circumambulated the column two times in one direction and three times in the other, acquiring an enormous smear (Fig. 5, 6).