Final report

ECOLOGICAL AND MORPHOLOGICAL STUDIES ON SELECTED PLANTS

March 1998-December 2008

Prepared by
Hans Bänziger

Principal researcher
Dr. Hans Bänziger
Department of Entomology and Plant Pathology
Faculty of Agriculture
Chiang Mai University
Chiang Mai 50200
Thailand
Tel. (053) 944026 ext. 22; Fax: (53) 944666
e-mail <sangda.h@chiangmai.ac.th>

Co-researcher
Mr. Prachaval Sukumalanan
Department of Entomology and Plant Pathology
Faculty of Agriculture
Chiang Mai University
Tel. (053) 944029; Fax: (53) 944666

Collaborator
Dr. Chaweewan Hutacharern
National Parks, Wildlife and Plant Conservation Department
Bangkok

Publications added separately


1. **BACKGROUND AND RATIONALE**

Results of the previous Project (FLOWER POLLINATION, MOTH ZOOPHILY AND PHYTOPHAGY: APPROACHES TOWARDS THE PROTECTION OF RARE AND COMMON SPECIES, 1992-1997) highlighted two most interesting plant groups: lady slipper orchids (*Paphiopedilum* spp.) (Orchidaceae) and rafflesias (*sensu lato* [s.l.]), which comprise the genera *Rafflesia*, *Rhizanthes*, and *Sapria*, (Rafflesiaceae). Both are aesthetically exceptionally beautiful and/or odd-looking. Moreover, their biology, especially the pollination syndromes, are of no lesser interest due to their unexpectedly high level of sophistication: they are deceptive flowers which cheat insects to pollinate them without offering them any reward, or ever induce them to commit ‘infanticide’.

Also, both are more or less rare which is in part ‘natural’ but in good part man-caused. Such rarity has both a serious drawback and at the same time is also cause for deep concern. The drawback is that because of their rarity they are very difficult to study, so that only little has become known about their biology in the wild state. The concern is about the chances of their survival in nature since they are so rare. The two features are linked because their rarity cannot be understood, nor can appropriate conservation measures or programs be formulated, when the plants’ ecology and biology in the natural environment are not, or only insufficiently known.

From the studies I have so far conducted, it appears that the level of, and reason for, their being endangered is different in slipper orchids and rafflesias s.l. Slipper orchids, while being naturally rare (except possibly in certain restricted habitats) due mostly to low fruit production and extremely specific habitat requirements, are endangered mostly by human activity. Their present-day dire predicament is mainly the result of their being collected, as **whole** plants, for the trade of live ornamentals. Rafflesias’ natural rarity appears to have its roots essentially in their inability to reinfect frequently enough new host lianas, besides low fruit production. The main man-caused threat is habitat loss. As yet they cannot be cultivated but even when this will be possible in the future, few people will be interested in having a fetid, only briefly flowering plant in their home, so that they are not expected to be endangered by the trade of ornamentals. Also, when they are
collected, e.g. as ‘medicinal’ plants or as tourist curios, then often only the flower, or in
the worst cases also the adjacent root, is collected while the vegetative parts of the plant
inside the host liana remains alive and can flower again next season, unless too much
damage has been done to the roots of the host. The tourist trade, especially the so-called
‘eco-tourism’, though, is rapidly increasing pressure on the habitat and will soon become
a major problem unless it is kept reasonably restricted. The major damage by ‘eco-
tourism’ is the trampling of buds unseen beneath the leaf litter, resulting in their abortion,
in addition to the clearing of the vegetation to ease passage, and the cutting of lianas
(often the hosts of rafflesias s.l.) to drink the water contained in the stem, a frequent
bragging act by tourist guides to show off the ability to ‘survive’ in the forest.

2. OBJECTIVE AND SCOPE

Such outstanding creations of nature – their aesthetic beauty and even more their bio-
logical sophistication – deserve to be better known and appreciated by man simply on
account of their being such marvels. At the same time it is hoped that this will temper
man’s greed and foster his respect for these creations. This leads to the second objective
of the project, namely the conservation of these marvels for posterity. Their continued
existence in the future depends on the correct understanding of their ecological require-
ments. This can only be acquired by detailed studies, especially those carried out in
their natural habitat. Without such knowledge, no appropriate protection measures can
be formulated for the safety of these threatened marvels.

3. METHODOLOGY AND TECHNIQUES

In order to watch the pollinators’ activity at epiphytic flowers of the lady slipper
orchid *Paphiopedilum parishii* growing in the tree canopy, the method to climb trees
was the same as for *Paphiopedilum villosum* (studied in the previous project) which can
grow up to 35 m above ground. With the help of a powerful bow a special, rather heavy
arrow (self-made from an iron tube) was shot over a branch below which an orchid
clump grew. At the end of the arrow a fine fishing line was attached. After retrieving
the arrow which fell down well beyond the branch with the attached line, this was then
used to draw up one or more, each time stronger line until a mountaineering rope could
be drawn up. This was finally used to climb the tree with ascenders, sitting harness, etc.
It is a tiring and time-consuming activity.

More details on methods are mentioned in the respective sections. The principal
researcher mostly worked alone. This was in order not to reveal to potential poachers the
sites of endangered plants.

4. RESULTS

4.1. Studies on the natural pollination of wild lady slipper orchids: *Paphiopedilum
callosum, P. parishii* and *P. bellatulum*

Whereas the study of the pollination of the slipper orchid *Paphiopedilum villosum*
(Lindl.) Stein has been concluded already during the previous project, the species *P.
charlesworthii* (Rolfe) Pfizter, *P. parishii* (Rchb. f.) Stein, *P. callosum* (Rchb. f.) Stein
and *P. bellatulum* (Rchb. f.) Stein, had generally been studied only preliminarily. A main
object of this part of the project was the study of the latter ones.
P. callosum was studied in the Khlong Nakha Wildlife Sanctuary. A one-day trek was necessary to reach the study sites. Porters were necessary to carry the camping gear and food for several days' stay near the study sites. Mr. Supharb Nakul, head of the nearest substation, was instrumental both in showing me the orchid sites by coming along with me, and by organizing the porters.

The study population was in secondary evergreen forest at 950-1080 m a.s.l. and consisted of 24 clumps over a distance of about 4 km. The flowers were watched for a total of 53 hours over two years. The species flowered in late March. The flowers were odourless to my nose. The pollinator turned out to be the females of the hoverfly Episyphus alternans (Maquart) (Syrphidae, Diptera). They were evidently attracted by an allomone produced by the orchid mimicking an odour released by a colony of aphids, the prey of the progeny of the hoverfly, since this laid an egg, mostly on the staminode, every time it visited the flower. But, a few seconds after landing, the hoverfly lost its grip and tumbled into the pouch (lip) opening of the orchid, where the insect remained temporarily prisoner. While the young hatchlings were doomed to starvation because no aphid prey was present on the orchid, their mother could escape imprisonment by climbing up the hind wall of the orchid. There a channel leads past the stigma where a potential pollen smear acquired by the fly during a previous visit of an orchid would have been smeared off. Advancing further up, the hoverfly had to force itself out of the narrow exit gap to obtain freedom. While extruding itself out of the gap it scooped off a pollen smear from the anther strategically positioned at the exit. The pollination system is evidently a clear case of brood-site deception.

On inspection, some 40% of the flowers had a pollen smear on the stigma (checks done without damaging the flower). If extrapolated for a presumed flowering period of five weeks, fruiting could have been expected in some 90% of the flowers.

Paphiopedilum parishii was studied in the Doi Chiang Dao Wildlife Sanctuary at a site I had discovered myself. From the base camp a very steep, slippery two-hours trek was necessary to reach the site. In certain years I bivouacked at the study site for several days in a row. Since the species is generally epiphytic, I had to climb up the trees with ropes. Very sadly this site was plundered by poachers and the orchid was nearly exterminated already before I had been able to conclude my study.

The flowers were watched for pollinators for a total of 104 hours over 5 years. The main pollinator was found to be the females, rarely the males, of the hoverfly Allograpta robinsoni (Curran). However, this hoverfly never laid eggs, hence the attraction must have been based on lures other than brood-site deception as found in P. callosum, but probably enacted by a combination of alighting suitability, central location, colour combination, and odour emission. Capture of the pollinator occurred again when the hoverfly slipped off the staminode a second or two after landing on it. Pollen acquisition and delivery was as in P. callosum. P. parishii probably deceives by food-dissimulation.

Fruit formation was in 9-58% of the flowers.

Paphiopedilum bellatulum was also studied in the Doi Chiangdao Wildlife Sanctuary where it is a calcicole species clinging to limestone cliffs. During 11 years 14-89 plants were surveyed, the lower number again being due to poaching. Each year about half of the plants flowered. Flower watching for pollinators totalled 136 hours over nine years.

The pollinator proved to be the hoverfly Eumerus splendens Wiedemann. The mechanical aspects of the pollination was again similar as in the above two species, but the lure at work is not yet fully understood but at any rate no eggs were ever laid. E.
splendens belongs to a different subfamily of hoverflies - the Milesiinae - from the above-mentioned hoverflies which are all Syrphinae. The larvae of the Milesiinae are not aphid-predators but are phytophagous or saprophagous. Unfortunately, the larval feeding habits of tropical Eumerus are not known, hence we cannot be sure about the lure working in the flower. We only can tentatively assume that the orchid somehow dissimulates, olfactorily and possibly visually, the food source of adult females or their progeny.

Fruit formation was in 41-92% of the flowers.

In P. charlesworthii long-distance lure appears to be the showy sepal, but its pinkish violet colour apparently also mimics that of reward-offering flowers of similar colour, such as Camchaya loloana Kerr, Boea glabrisepala (Burtt) Barnett, Dichiloboea birmanica (Craib) Stapf, and Clerodendrum urticifolium (Roxb. Wall. growing in the vicinity. Apis cerana bees were repeatedly seen flying to the orchid after visiting such flowers, but then always flew away from the orchid without attempting to alight. Close-range attraction is by the striking white staminode and its yellow-tipped protuberance towards which the pollinator flies. Capture and escape are as in P. villosum. The flowers are rarely visited by pollinators and despite many hours of flower watching during many years, only two cases of pollen acquisition were observed, one by Episyrphus alternans and one by an undescribed species of a new genus near Meliscaeva. It is the region’s most threatened slipper orchid, with an alarming low rate of fertilization of 0-2%, i.e. a nine-year average of 0.67%, when 15-318 flowers were censused.

References

4.2. Studies on the taxonomy, morphology, biology and ecology of Rafflesiaceae

Morphology and taxonomy
Since for the study of the pollination there is need to know exactly the structure of the flowers involved, this also means that one gains a thorough understanding of the morphology and hence the taxonomy of the flower. This is particularly true for the highly reduced, parasitic Rafflesiaceae which essentially consist only of the flower. The author found many inconsistencies in the taxonomic treatment of many Rafflesiaceae. An overall taxonomic re-evaluation of species in the genera Sapria and Rhizanthes was urgently needed. The late Dr. Bertel Hansen, Copenhagen University, Denmark, a Botany taxonomist who had formerly treated the Rafflesiaaceae of Thailand, joined in as co-author. Because these genera are distributed also in neighbouring countries, it was necessary to travel to Java, Sumatra and Borneo to carry out field and herbarium research there. A grant by the British Ecological
Society of 1000 GBP helped covering much of the author's expenses. This resulted in a taxonomic revision of one genus with new circumscriptions and redescriptions of species, as well as descriptions of four new taxa.

These unexpected results are not only important for Botany, but are a prerequisite for the second part of the project, namely the study of the ecology of these species. Without exact recognition and names of the flowers to be studied, no proper ecological research can be carried out.

Taxonomic results

*Sapria poilanei* Gagnepain had been very misleadingly described; we re-described it as *Sapria poilanei* Gagnepain emend. Bänziger & Hansen, with the female flower being described for the first time.

Another, somewhat similar species has been confused with *Sapria poilanei* and with *Sapria himalayana* Griffith, or went otherwise unrecognized, so that we described it as a new species, *Sapria ram* Bänziger & Hansen.

A further taxon, found in northeast Thailand, was often confused with *Sapria poilanei* due to its white spots, or wrongly assumed to be the same as *Sapria himalayana*. We showed that it evidently is an infraspecific taxon of *Sapria himalayana* and described it as *Sapria himalayana* Griffith forma *albovinosa* Bänziger & Hansen.

We found that *Rhizanthes* was even more confused and carried out a taxonomic revision of the whole genus. We showed that the two hitherto known, not reliably separable species of *Rhizanthes* actually consist of at least four species: *R. zippelii* (Blume) Spach from Java, *R. lowii* (Beccari) Harms from Borneo, the new species *R. deceptor* Bänziger & Hansen from Sumatra, and another new species, *R. infanticida* Bänziger & Hansen from southernmost Thailand, Peninsular Malaysia and Sumatra.

*Rhizanthes lowii* was studied during a separate mission to Borneo in 2006. It was discovered that this species can also have bisexual flowers, like *R. zippelii*. Bisexual flower were described for the first time in *R. lowii*, together with fruits and seeds which were also unknown previously.

For more details see References.

Biology and ecology

While flowers of Rafflesiaeaceae are notoriously rare, information on their fruits are even more scant. The first fruit of a *Rafflesia* and a *Rhizanthes*, two of the three genera belonging to this family, became known to science only some 20 and 80 years after their flowers were described, respectively. The mature fruit of *Sapria*, the third genus of the family, has remained unknown for nearly 160 years, namely until it was discovered in the course of the present research. Mature fruit and seed of *Rafflesia kerrii* were also unknown before this study.

It was demonstrated that the flowers of *S. himalayana* are not apomictic but rather require pollination for fruit set (Bänziger, 2004). The development of the ovary, ovules, fruit and seeds is documented descriptively and photographically from anthesis until the natural splitting open of the mature fruit 5-6.5 months later. The fruits of *Sapria* and *Rafflesia* clearly differ in many aspects. They are fissured berries: blackish, flattened barrel-shaped, 21-32 cm in circumference and 3.1-5 cm long in *S. himalayana*, but red-brown, truncated cone-like, 40-51 cm in circumference and 7.5-11.5 cm long in *Ra. kerrii*. The minuscule seeds, however, are very similar, 0.6-0.65 mm by 0.29-0.33 mm in *S. himalayana*, a third larger in *Ra. kerrii*. If not protected, all fruits were eaten by rodents, probably wild rats and squirrels, the presumed seed
dispersers. In experiments, rats consuming a whole fruit passed some 15,000 undamaged seeds in their fecal pellets.

A technique to manually pollinate Sapria, Rafflesia and Rhizanthes was devised (Bänziger, 2004). It uses appropriately bent aluminium strips to reach the concealed sexual parts of the flower to acquire and deposit pollen, after excising parts of the flower in some species. The fruiting rate of S. himalayana was thereby increased to 78% from 8-12% found in naturally pollinated populations. Thanks to this 6-10 fold increase in fruit set achieved by manual pollination, the method is not only important for yielding abundant fruit and seed for research but, most importantly, it is an effective new tool for the conservation of endangered Rafflesiaeaceae. This can be achieved in two ways: one is to increase fruit set by manually pollinating flowers in suitable populations and let nature take care of subsequent steps. The other is to devise techniques to enhance host infection. However, for this it will be necessary to crack the mystery of how Rafflesiaeaceae infect their hosts.

Whereas natural fruit set in S. himalayana was just 8-12%, in Rafflesia kerrii it was estimated at 20-30%. Essentially this is due to the far more abundant pollinator visitation of the latter compared to the former, viz. at least one fly throughout much of the day to up to peaks with 20 flies simultaneously in Rafflesia kerrii, but only one fly every 0.5-4 hours in S. himalayana.

Pollinators of Sapria himalayana himalayana were mainly female Lucilia porphyrina (Calliphoridae), other flies being only rarely involved, as were the males. Sapria himalayana forma albovinosa was pollinated mainly by Chrysomya pinguis (Calliphoridae), whereas in Sapria poilanei the pollinators were mainly Lucilia papuensis (Calliphoridae). The pollination of Sapria ram (more details further down) turned out to be exceptional as it was carried out by 11 species of Sarcophaga flesh flies (Sarcophagidae, not Calliphoridae) (in some other study areas possibly also by blow flies such as Chrysomya defixa).

Pollinator frequency during the flowering period of S. himalayana, September-April, was not constant. During the cool season, or about the second half of November to January or early February, pollinators were far less common than during the last period of the rainy season and during the hot season. Nevertheless, because there are many more flowers of S. himalayana during the cool period, and because their flowers last longer in that period, the contribution to the flowers’ reproduction in the cool season is probably comparable to that during the other two periods. In fact, during the rainy season the flowers’ viable period is shorter than in the cool season due to the rains which often flood the flower, and because they tend to become more mouldy on account of the persistent humidity. In the hot season, on the other hand, the viability of the flower is reduced by the air dryness which leads to water loss from the flower. Due to this the flowers tend to become flabby, the stigmatic fluid to dry up faster and the pollen mush getting thicker or dry to some extent. These conditions negatively affect successful pollination and subsequent fertilization. In the end, therefore, pollination during the three periods may be similarly successful.

Another important information about the reproduction is to know how the flower copes with the rainy season. A long, strong downpour can completely fill up the whole tube of the flower and overflow it. Completely water-logged flowers are no rarity during the rainy season. The disk with anthers or stigma are completely submerged and the flower is reproductively dead. However, to some extent the flower is protected against small rain by the diaphragma and the disk which act somewhat like an umbrella, since the anthers and stigmatic fascia are situated below it. Nevertheless, if too much rain assembles at the bottom of the tube, pollinators are likely to be deterred
from advancing deep enough into the flower to acquire or deposit pollen. Rain can affect reproduction in one more way, namely if rain falls after successful pollen deposition has already taken place in the female flower during fine weather. Again, a small shower will not wash off the pollen because the stigmatic fascia is protected below the disk. But a long downpour can submerge it. Nevertheless, presumably if water-logging occurs sufficiently long after pollination took place, by that time the pollen will already have germinated and the pollen tubes penetrated deep enough into the stigmatic tissue to remain unaffected by external water, thus being able to continue their growth, reach the ovary and fertilize the ovules. Completely water-logged flowers have been observed to develop normal fruit to maturity. To assess this scenario, manual pollination was carried out (technique as detailed above) with flowers which were then flooded artificially with water after various time intervals. Results indicate that, depending on seasonal temperatures, fruit and seed can develop normally if rain submerges the disk not earlier than five to seven days after pollination occurred.

Pollinators carry very variable amounts of pollen on their back, from much less than what is present at one anther of a male *S. himalayana*, up to an amount equal to several times of what is present at a single anther. Each flower has 20 anthers and flies often touch more than one anther upon entering or crawling around the circumambulator, thus acquiring more pollen than what is present at a single anther. They may also visit several male flowers before entering a female one. Thus, it would be interesting to know the minimal amount of pollen required for successful pollination of a flower and its subsequent development of a fruit. To this end experiments with manual pollination were again carried out using different fractions of the amount present at one anther. Results indicate that an amount of far less of what is present at a virgin anther, viz. down to about 1/15 of it, lead to the development of a normal fruit with seeds.

The pollination system of *Rhizanthes deceptor* was studied for the first time in Sumatra. It was found to be a typical exponent of a system which I termed as ‘opportunistic brood-site deception’ which is not as nefarious as the ‘perfidious brood-site deception’ found in *Rhizantes infanticida*. This latter induces its pollinators, some 10 species of blowflies (mainly *Lucilia* and *Chrysomya*, Calliphoridae), to lay up to 1000 eggs. The hatchlings will all end up dying from starvation because in reality there is no food for them. The flower only mimicks the odour, colour and, by its dense hair cover, the texture of a mammalian cadaver, the natural oviposition site for blowflies. *Rhizanthes infanticida* is the most pernicious of all flowers known to be pollinated by brood-site deception. The mode of pollen uptake and delivery has been detailed in a previous paper (Bänziger, 1996).

*Rhizanthes deceptor* has only a sparse, bristly hair cover which the pollinators evidently do not perceive as an appropriate oviposition site and are not mislead into laying any eggs. Hence no damage is inflicted to the progeny of the pollinator which ultimately is an advantage also for the flower. The mode of pollen uptake and delivery is as in the above-mentioned species. The pollinators were *Chrysomya defixa*, *Lucilia porphyrina* and *Hypopygiopsis fumipennis*.

Pollination in *Rh. lowii* from Borneo was similar to that of *R. deceptor* because it is similarly rather coarsely haired. In bisexual flowers selfing occurs more or less automatically when a pollinator leaves the circumambulator, or re-enters it, which occurs quite frequently. But cross-pollination can also occur when the pollinator carries pollen from a first flower to another one. The main pollinator at the study site was *Hemipyrellia ligurriens* (Calliphoridae). When unisexual flowers are involved, generally cross-pollination occurs.

References


4.3. Studies on the taxonomy, behaviour, feeding and reproduction of flesh flies (Sarcophagidae) in view of their role as pollinators of Rafflesiaceae and some Orchidaceae

Since the unexpected finding that the newly discovered raffesiaceous flower Sapria ram is pollinated not by blow flies (Calliphoridae) as all other Rafflesiaceae, but by flesh flies (Sarcophagidae), it was necessary to study this fly family in more detail. The taxonomy and identification of flesh flies is highly technical and there are only very few specialists in this field in the world, one being Dr. Thomas Pape, Natural History Museum, Stockholm, Sweden. Females generally cannot be identified and males can be identified with certainty only by their genitalia. Since only females are pollinators in S. ram, it was necessary to breed the progeny of the females involved to obtain males for correct identification of their mothers. The breeding was carried out by Bänziger in Thailand. This is a very time-consuming method. It is also a most unpleasant method because the breeding media needed are foul smelling. But it was unavoidable because there is no alternative method. The research resulted in three original publications as mentioned below.
46 species of *Sarcophaga* were found throughout Thailand during the study period. About 50% of the species were new to Thailand and some 10 new to science. Of the latter, 5 species have been described as new species, viz. *Sarcophaga krathonmai* Pape & Bänziger, *Sarcophaga saprianovae* Pape & Bänziger, *Sarcophaga circa* Pape & Bänziger, *Sarcophaga lanna* Pape & Bänziger, and *Sarcophaga suthep* Pape & Bänziger. 6 of the species already known from elsewhere but new to Thailand have been identified as *S. annandalei*, *S. hui*, *S. konakovi*, *S. situliformis*, *S. urceola*, *S. walayari*. The remaining 9 species new to Thailand cannot as yet be named because caught only in the females sex, which are nearly always unidentifiable in the tropics.

523 broods of *Sarcophaga* were reared. Rearing yielded three very important data. First, it ensured correct species identification through the male progeny (male genitalia structure) of the otherwise mostly unidentifiable females. Second, rearing also allowed several new correct male-female associations (from male and female progeny of the same mother), viz. *S. annandalei, S. harinasutai, S. multivillosa, S. ostindicae, S. yunnanensis*,  S. sp. 154. Third and most important, rearing offered new insights into the flies’ breeding strategies. The study proposes, for the first time, the distinction of three oviposition strategies: either laying on faeces, or on cadaver, or on both of them. For these strategies three new terms were coined: (1) coprobiodotic, (2) necrobiodotic, and (3) amphibiodotic, respectively. Examples for (1) are *S. africa, S. albiceps, S. misera*; for (2) *S. krathonmai, S. nathani, S. notabilis, S. peregrina, S. saprianovae*; and for (3) *S. annandalei, S. dux, S. ruficornis*. However, larvae of copro- and necrobiodotic species experimentally transferred to cadaver and faeces, respectively, also developed to normal adults.

Rearing was also done to obtain insight in the breeding behaviour of these flies. This is a prerequisite for a correct understanding of the lure with which flowers are able to attract and induce the flies to pollinate them. From previous and present field observations, *Sapria ram* (Rafflesiaceae) is pollinated by 11 species of *Sarcophaga* (for details see Bänziger & Pape, 2004). From field experiments with flowers of this species, it was found that it evidently mimics the odours of a cadaver rather than that of faeces. Further, the pollination system of *S. ram* is evidently based on both brood-site deception as well as food deception, but the deception at work during a particular pollination event depends on whether a necro- or coprobiodotic pollinator is involved. On a necrobiodotic *Sarcophaga* it works by brood-site deception, but on a coprobiodotic *Sarcophaga* it acts by food deception.

13 species of *Sarcophaga* are also the pollinators of the orchid *Bulbophyllum putidum* studied in a home garden (details see Bänziger & Pape, 2004). Interestingly, both males and females were involved in the pollination, unlike *Sapria ram* where only females are pollinators.

The unexpected laying chosiness between excrement or carrion in the wild is discussed, together with the role played by laying habits in myiases (diseases caused by adult flies), animal as well as human.

**References**


Bänziger, H. & T. Pape. 2004. Flowers, faeces and cadavers: natural feeding and
laying habits of flesh flies in Thailand (Diptera: Sarcophagidae, Sarcophaga spp.). *Journal of Natural History* 38: 1677-1694.

### 4.4. Studies on *Tetrastigma* pollination

Knowledge of the pollination of *Tetrastigma* (Vitaceae) is important because several of these lianas species are hosts to Rafflesiaaceae. The study involved *T. harmandii* and *T. hookeri*, the main hosts of *S. ram*, and non-hosts *T. baenzigerii* and *T. curtisi*. The first three were studied in a garden at the foot of Doi Suthep, the latter in the Doi Suthep NP. The latter flowered December-January, *T. harmandii* and *T. hookeri* in February, *T. baenzigerii* April-May. The flowers are small, yellowish-green, pleasantly fragrant. *Tetrastigma* are dioecious, hence male and female flowers are on different liana individuals. Insect visitation was studied mainly in *T. baenzigerii*, the largest of these lianas and with the most flowers. A wide variety of insect visitors were found, including many bee species from various families (Apidae and Halictidae), subfamilies and tribes, as well as wasps, butterflies, beetles, mosquitoes, carrion flies, bugs. However, most of them only steal nectar and/or pollen without effecting pollination. Even *Apis cerana*, *A. florea*, *A. andreniformis* are evidently not very efficient. Worse, they deplete pollen from the flowers which are too small, particularly in the case of *Apis cerana*, for effecting proper contact with the stigma. Stingless bees (Meliponini) are better adapted to act as vectors and sweat bees (Halictidae) are probably the most efficient pollinators of this liana, including *T. hookeri* and *T. harmandii*. However, they tended to be less frequent then *Apis* at the study sites, hence their actual contribution to pollination was less than as expected from their single capability. Among bees visiting *T. baenzigerii* and *T. hookeri* was a particularly interesting stingless bee, the minute *Lisotrigona furva*, unexpectedly discovered to exhibit unsuspected tear-drinking habits. This behaviour has been researched in detail, resulting in an important spin-off study which has been published separately as mentioned below.

### References