Taiwania 67(2): 201–210, **2022**
DOI: 10.6165/tai.2022.67.201

Strong emissions of carbon dioxide and water vapour by *Sapria himalayana* Griff. (Rafflesiaceae): waste or necessity in a cool flower?

Hans BÄNZIGER[1,*], Andreas GIGON[2], Saengdao BÄNZIGER[3], Piyawan SUTTIPRAPAN[1]

1. *Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand.* ***2.*** *Institute of Integrative Biology, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland.* ***3.*** *Department of Animal and Aquatic Science, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand. [*]Corresponding author's phone and email: Tel. (053) 944 062, ext. 16; hans.banziger@cmu.ac.th*

(Manuscript received 24 September 2021; Accepted 9 March 2022; Online published 23 March 2022)

ABSTRACT: Due to respiration, the carbon dioxide present in the sapromyiophilous flowers of *Sapria himalayana* in its forest habitat in N Thailand was found to be five to nine times that of the ambient air. On the other hand, the emanation of carbon dioxide from a cadaver, the volatiles of which the flower mimics in its pollination syndrome, was not higher than that of the forest soil and thus in the ambient air near the ground, suggesting that the carbon dioxide is not part of the mimicry. This, and our preliminary finding that the carbon dioxide had neither attractive nor anaesthetic effects on the flower's pollinators, the blowfly *Lucilia porphyrina*, indicates that the carbon dioxide essentially appears to be a waste by-product. Attraction is mainly by putrid volatiles. The water vapour in the flower's tube of *S. himalayana* was found to be constantly close to saturation, even during the dry season when ambient minima averaged 40% RH. This resulted in the unexpected finding that while the flower was slightly thermogenic in humid ambient during the rainy season as in other Rafflesiaceae, it was constantly slightly cooler than the ambient during the dry season due to strong water evaporation. High humidity inside the flower is essential because the pollen can be acquired by the flies only in a fluid suspension.

KEY WORDS: Blowfly pollinators, cadaveric volatiles, cooling, fly attraction, *Rafflesia*, respiration, transpiration.

INTRODUCTION

Rafflesiaceae are renowned for their gigantic flowers, their vegetative bodies growing holoparasitically concealed inside their liana hosts, and their pollination syndromes being among the most deceptive. The family has been reduced to three genera, viz. *Rafflesia*, *Rhizanthes* and *Sapria* (Takhtajan, 1997). From 18 species (Meijer, 1997; Nais, 2001) *Rafflesia* has now proliferated to over 30 species (e.g. Balete *et al*. 2010), while both *Rhizanthes* and *Sapria* have four species (Bänziger and Hansen, 1997, 2000; Tanaka *et al*., 2019). Most important recent studies of Rafflesiaceae are on biology and ecology (e.g. Elliott, 1990; Bänziger, 1995; Hidayati *et al*., 2000; Nais, 2001; Heide-Jørgensen, 2008), pollination (Beaman *et al*, 1988; Bänziger, 1996, Bänziger and Pape, 2004), fruits and seeds (Bouman and Meijer, 1994; Bänziger, 2004; Bänziger *et al*. 2007), cytology, development of vegetative body and floral organs (Heide-Jørgensen, 2008; Nikolov *et al*. 2014), and molecular genetics (e.g. Blarer *et al*. 2000; Barkman *et al*. 2004, 2008.; Davis *et al*. 2008; Nickrent *et al*. 2004; Bendiksby *et al*. 2010; Nikolov *et al*. 2013).

In the only two studies on physiology of the Rafflesiaceae so far, endothermy was discovered in the flower of *Rhizanthes lowii* (Beccari) Harms and *Rafflesia tuan-mudae* Beccari (Patiño *et al*., 2000, 2002). While this fascinating feature is found in some 13 other plant families (e.g. Seymour, 2010), two ideas by Patiño *et al*. (2002) are of particular interest in our context. First, by calculation they predicted a strong emanation of CO_2 in *Ra. tuan-mudae*. Second, Patiño *et al*. (2000) had suggested that CO_2, combined with other volatiles, might increase the probability of pollination in *Rh. lowii*, and possibly work as an anaesthetic. Previously, in a study of the pollination of *Rhizanthes infanticida* Bänziger & Hansen (as *Rhizanthes zippelii* (Blume) Spach), Bänziger (1996) had already mentioned that in a non-photosynthesizing plant, CO_2 is more in evidence (no O_2 production). Also, according to Barton Browne (1979), CO_2 is an oviposition stimulant (though not an attractant) in the fly *Lucilia cuprina* (Wiedemann) on live sheep (not on carrion).

The aim of this study is (i) to actually measure if *Sapria himalayana* emanates copious CO_2; (ii) to interprete the concomitantly found, constantly very high water vapour transpiration inside the flower; and (iii) to discuss, based on literature and some preliminary experimental data, whether CO_2 has an attracting and/or anaesthetic function in pollinators. We studied *Sapria himalayana* Griffith instead of *Rafflesia* or *Rhizanthes* because the nearest sites of the latter two are some 1000 km distant whereas the former grows in our region.

MATERIALS AND METHODS

Biological and ecological charasteristics of *S. himalayana*

Sapria himalayana is distributed over a vast area from the southeastern Subhimalaya to Indochina down to N, NE

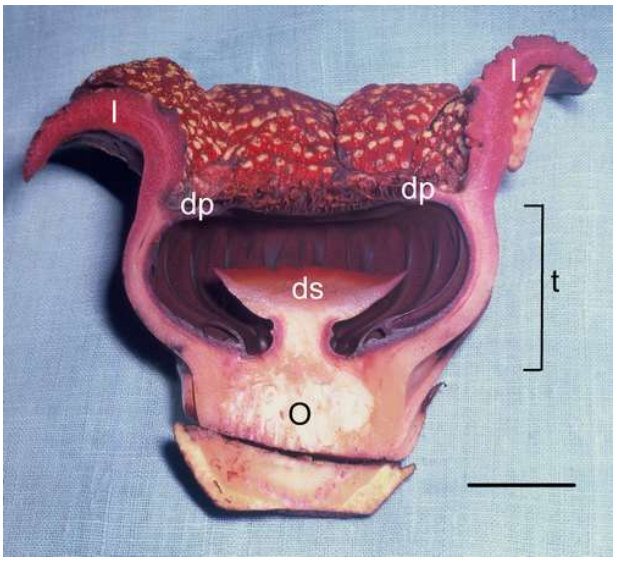

Fig. 1. Longitudinal section of a female ***Sapria himalayana***. Note the lobes (l), diaphragm (dp), tube (t), disk (ds), and ovary (o). Bar length 3 cm. Photo H. Bänziger.

Fig. 2. Female ***Lucilia porphyrina*** on the diaphragm of a female ***Sapria himalayana***, about to enter the inner part of the flower. Note the two yellowish crusts of pollen 'mush' on the thorax of the fly (acquisition from a male flower not seen). The crusts will be reliquefied and brush-sponged off on contact with the underside of the disk awash with stigmatic fluid. Photo H. Bänziger.

and NW Thailand, but only in few and very localized foci, hence its endangered status. Our study was with eight different clusters (a cluster is the buds and flowers parasitizing a single host), at three sites 0.5–1 km from each other, in the Doi Suthep National Park, Chiang Mai, N Thailand, at 1250–1300 m a.s.l., November and December 2006 (weather variable, mid-level humidity and relatively low temperature), March and April (hottest and driest), September and October (wettest), 2007. The habitat was a primary Hill Evergreen Forest in which the soil surface is always in the shade except when there are occasional sunflecks. *Sapria himalayana* is a holoparasite permanently concealed as filaments inside its host except when flowering. From its host, at our sites the large liana *Tetrastigma laoticum* Gagnepain (recently synonymized under *T. planicaule* (Hook. f.) Gagnepain (Trias-Blasi *et al*., 2020)) (Vitaceae), the parasite sucks nutrients through haustoria. The following descriptions are based on Bänziger (1996, 2004). Flowers appear only on roots of the host, in a radius of up to over 10 m around the host's stem entrance into the soil. The flowers, about 15–20 cm wide and 8–10 cm high, have its basal parts mostly slightly below, occasionally just above ground. The structure of the flower is shown in Fig. 1. Flowering occurs mainly between September and early April. Anthesis lasts 5–7 days. Flowers are unisexual. Usually both sexes are present in a cluster but the ratio is variable. The odour emanated by the flower reminds that of rotting flesh but, being much weaker than that of *Rafflesia* or *Rhizanthes*, requires close smelling. Pollen is presented as a yellow drop of mush-like consistency at the tip of 20 anthers set in a row around the underside of the disk. The stigmatic fascia on the underside of the disk is awash with clear fluid. Pollen is acquired as a smear on the back of the thorax of pollinator *Lucilia porphyrina* (Walker) (Diptera, Calliphoridae), mostly but not exclusively females, or very rarely other fly species, while circumambulating below the disk. The smear will dry to a crust in about one hour once the fly has left the flower. Viability of dry pollen is up to three weeks. On entering a female flower (Fig. 2), the smear is quickly reliquefied by fluid-soaked papillae of the stigmatic fascia and 'brush-sponged' off (Bänziger, 1996, 2004). It should be mentioned that Nais (2001) found the viability of dry pollen to last less than 3.5 days in *Rafflesia pricei* Meijer, but his pollen germination experiments were with an artificial medium *in vitro*, whereas the former's experiments were *in situ* on live stigmas.

Measurement of CO_2 and H_2O emissions of *Sapria* flowers, soil, and the skin of a dead rabbit

The emissions of CO_2 and H_2O of the *Sapria* flowers (i.e. their respiration and transpiration), of the soil near the latter, and of the skin of a dead rabbit, were measured with the battery operated LCpro+ Photosynthesis system combined with the SRS-1000 Soil Respiration System, both of ADC BioScientific Ltd., Hoddesdon England. Fig. 3 shows the transparent measuring chamber placed over a *Sapria* flower and the red 'umbilical cord' leading the data to the measuring and steering console.

Measurements were carried out between the middle of November and the beginning of December. Preliminary trials had shown that the gas exchange of *Sapria* was strongest during midday and early afternoon. Therefore, the measurements were made during that period, when the environmental conditions around the flowers were as follows (about 10 cm above the soil surface): 16.9–20.8°C, 77–90% RH, 361–399 volume ppm CO_2, photosynthetically active radiation ≤17 µmol/m^2 sec (i.e. 0.1–0.2% of full sun light), atmospheric

Fig. 3. As shown in the upper right, a transparent measuring chamber is firmly placed over a ***Sapria himalayana*** flower and sealed with aluminium foil. The chamber contains a fan and sensors for air temperature; the handle has an infrared gas analyzer for measuring the concentrations of CO_2 and water vapour. A red 'umbilical cord' leads the measured data to a console with a battery, a display screen, and a microprocessor. The latter automatically controls the parameters in the measuring chamber and performs the calculations of respiration and transpiration. Special sensors (not shown) measure ambient air temperature and humidity as well as air pressure. Photo A. Gigon.

pressure 881–889 mbar. All these data were assessed with the instrument mentioned above.

The transparent measuring chamber (without the steel collar) was placed over the flower from which one or two lobes had been cut off, so that the fan in the chamber could work properly. The wounds were covered with Vaseline to prevent water and turgor loss. Removing one or two of the ten lobes, i.e. 2–3% of the flower's tissue biomass, do not much influence its gas exchange (see section Respiration of different parts of *Sapria* flowers). The base of the flower covered less than half the soil surface in the chamber. To prevent that the small amount of additional CO_2 from the (small) soil respiration was measured simultaneously with that of the flower, the soil was covered with aluminium foil. Furthermore, we always took care to inhibit any gas leaking in or out of the chamber by sealing the rim of the chamber with crumpled aluminium foil (Fig. 3).

The LCpro+ instrument functions as an 'open system' with an air flow (of 100 µmol/sec set by the factory) through the measuring chamber (Fig. 3) containing the plant or object to be measured. The volume of the chamber is 999 cm^3 (basal area 111 cm^2; height of 9 cm). The CO_2 and H_2O concentrations of the air entering and leaving the chamber are measured with a miniaturized infrared gas analyzer (IRGA) placed in the handle of the instrument (Fig. 3). Stable values were reached about half an hour after the chamber had been put in place. Calibration of the CO_2 and H_2O measurements are performed automatically by a microprocessor placed in the steering console (the zeroing for CO_2 is automatically made by passing the air flow over small NaOH pellets, and for H_2O over drierite). The influence of variations in temperature and atmospheric pressure on the gas exchange values measured is automatically compensated by the microprocessor in the steering console. A circulatory fan inside the measuring chamber ensures a good mixing of the air (inhibiting problems concerning boundary layer resistance). Water never condensed on the flower in the measuring chamber.

Experiments of sucking air directly from the tube of the flower and measuring its CO_2 concentration with the IRGA showed that in this inner part of the flower 2250 to 3340 vol ppm CO_2 were reached.

The soil respiration was always measured in-between the measurements of the *Sapria* flowers, i.e. under very similar environmental conditions and at a distance of less than 3 m from the flowers. Loose litter on the soil surface was removed and the chamber firmly placed directly on the undisturbed soil surface, i.e. without the metal socket provided for that purpose (data were recalculated accordingly). The chamber was never placed on sites with stones >1 cm in diameter or plant roots on the soil surface.

In order to compare the emanation of CO_2 from *Sapria* with that from a cadaver (the model the flower mimics to attract pollinators), a dead rabbit was used. It was placed on a table below a roof at a building of the Faculty of Agriculture of Chiang Mai University. The chamber was placed firmly onto the rabbit's abdominal flank, with weights to improve contact. Measurements were carried out 12 h, two, four, and six days after its death.

Calculations of the CO_2 and H_2O emissions

The LCpro-Instrument is conceived for measuring gas exchange of flat surfaces (leaves). If a fleshy flower is measured, the chamber's volume is reduced and thus the measured values are too high. These must be corrected. The average volume of a female and a male *Sapria* flower is 184.5 cm^3 and 155 cm^3, respectively (see Results of laboratory measurements of flower dimensions). Thus the data given by the instrument are 184.5/999=18.5% and 155/999=15.5% too high for female and male flowers, respectively. The data shown in Tables 1 and 2 have already been adjusted accordingly. The gas exchange of different parts of the flower (Table 2) was assessed by covering some parts of the flower with Vaseline.

Our data on CO_2 and H_2O emissions are expressed in the well-known unit µmol CO_2/m^2sec and µmol H_2O/m^2sec, respectively, i.e. relative to the surface area. This allows direct comparison of the gas exchange rates between the *Sapria* flowers, the soil, and the skin of a dead rabbit. Unfortunately, because of the rarity of *Sapria*, not many measurements could be carried out. Therefore, it was not possible to obtain enough data for detailed statistical analyses, except for calculating the standard deviation.

Measurements of temperature and humidity in the *Sapria* flowers during the dry and the rainy seasons

The temperature was measured in the center of the flower, i.e. in the disk and its stalk. The pin with the sensor of the thermometer (TFX 430 Pt100, resolution 0.02°C, of Ebro Ingolstadt, Germany) was inserted into the disk, vertically down for 0.5–1.0 cm. Although the cooling effect by transpiration occurs mainly at the surface of the transpiring tissue, we expected it also inside the disk. In fact, being flattish it has an upper and lower surface, and is supported by the stalk (itself with much surface area) attached to the base of the tube. Hence the sensor's position was closely surrounded by surfaces and thus expected to give data essentially equivalent to the surfaces. The stick with the sensor of the hygrometer (605-H1; resolution 0.1% RH, of Testo, Lenzkirch, Germany) was introduced diagonally into the space below the diaphragm but above the disk, and advanced to nearly reach the tube wall of the flower, without touching any surface. Hence the sensor was in the space of the water vapour present in the tube. Being lighter than dry air, the water vapour will leave the tube through the aperture of the diaphragm. Thermometer and hygrometer were left in their position throughout the measuring sessions. Ambient humidity and temperature were measured with additional Ebro and Testo sensors hung up near the flower, some 10 cm above the soil. Measuring sessions lasted at least 4 h, readings were made every 5 min.

Laboratory measurements of *Sapria* flower dimensions

Two male and two female *S. himalayana* flowers from the alcohol preserved collection at the Department of Entomology, Chiang University, were drained. Following treatments were made. (1) Each was then weighed. (2) The plant tissue volume was measured by the liquid displacement of each flower when immersed in alcohol. (3) The tube's inner free (space) volume (Fig. 1) was measured by the amount of alcohol needed to fill the space up to the diaphragm after draining. (4) For the surface area of the flower, the perigone lobes were cut off and measured separately. The outer surface of tube and lobes was not considered because it is smooth, glossy and relatively hard and thus has only a relatively small gas exchange, as indicated by the respiration of a bud in Table 1. The more or less flat surface area of the 10 lobes was assessed by drawing each silhouette on millimeter paper and counting the mm squares enclosed by the drawing. The average inner surface of a single lobe was 16.4 ± 3.5 cm^2; the ten lobes thus had an average total surface of 164 cm^2 (the overlap of the lobes was not more than 5%). This was more than the ground surface of the measuring chamber, i.e. 111 cm^2, because the lobes were inclined. For assessing the inner surface of the flower's tube, this was cut vertically in five equal parts. These were relatively flat and could be measured as done with the lobes, which enabled to calculate the surface of the whole tube. The area of the circular diaphragma and of the disc was obtained by measuring their diameter. The area of the disk was counted twice because it has an upper and a lower surface, set as it is within the tube, unlike the diaphragm whose outer surface is outside the tube. The inner surface area in males is slightly larger than in females because in these the ovary takes up part of the flower base. So we took the average, i.e. 106 ± 9.6 cm^2. (5) For assessing the dry weight of the flowers, silicagel was used as desiccant.

Experiments with fly attraction

The following observation (Bänziger, unpublished) indicate that sight is not required for pollinating flies to locate *Sapria* flowers: Blowflies *Lucilia sinensis* Aubertin and *L. papuensis* Macquart were seen crawling below the natural stratum of leaf litter in a forest in SE Thailand; removal of the leaves revealed a *Sapria poilanei* in full flower previously concealed by leaves. This led to following experiments to detect whether decomposition odours or CO_2, alone or in combination, can attract pollinators.(6) A dead rat (*Rattus rattus* (L.)) and a piece of smelly liver were brought to two different sites on Mount Suthep for separate observation. After having been completely covered with leaf litter they were watched for flies for an hour. (7) A *Rafflesia kerrii* flower (in S Thailand), was covered by two sheets of green mosquito netting so that the flower was not discernible but volatiles could escape. (8) The attractiveness of CO_2 to pollinators was assessed with 0.5 kg of evaporating dry ice and compared to pork meat and liver, 50 g each, mildly and strongly smelly, respectively, at the research sites on Mount Suthep but not in the vicinity of *S. himalayana*. These baits were exposed in three open plastic boxes (10 cm diameter, 7.5 cm height) individually covered by green mosquito netting. They were sealable with a screw-on cap when odour emission had to be prevented. The dry ice box was placed 2 m down- or upwind (air movement was very slow) from the other two boxes which were near each other. Every 15 min the CO_2 box was swapped with both, the meat and liver boxes. After an interval of 15 min the meat and liver boxes were sealed for 15 min, but the CO_2 box was never closed. The whole swapping process was then repeated, two times with the boxes in line with the wind flow, and two times by placing them across the wind flow. The flies settling on the netting of the boxes were counted but not collected.

In order to assess a possible role of CO_2 in causing anaesthesia in flies, the following experiments (9, a–c) were carried out. One female *L. porphyrina* was released into the tube of one of four freshly opened *S. himalayana*. The aperture was then immediately closed by a) a gauze (mesh width 1 mm), b) a gauze (mesh width 0.2 mm), and c) a transparent plastic sheet, air-tight sealed to the diaphragm

Table 1. Respiration and transpiration rates of flowers and a bud of ***Sapria himalayana***. Acronyms in the first column refer to the cluster site and flower index of ***S. himalayana*** studied on Doi Suthep, N Thailand. Asterisk*: flower scenescent.

Site	Date	Time	Sex	Days since flower open (unless bud)	Number of lobes cut off	Respiration µmolCO_2/m^2sec	Transpiration µmolH_2O/ m^2sec	Ambient air humidity RH%	Ambient air temperature°C
D3a	14 Nov.	14:40h	♂	≤ 1	1	11.7	67	87	20.3
D3b	14 Nov.	16:13h	♂	> 3	0	5.5	51	85	20.7
D3c	14 Nov.	16:39h	♂	> 10*	4	≥ 3.7	43	85	20.8
D3d	14 Nov.	15:47h	?	bud	0	2.4	44	81	21.3
B10	22 Nov.	15:15h	♀	3-4	2	17.7	57	81	17.5
D3a	24 Nov.	13:55h	♀	0.5-1	1	32.1	122	77	17.4
D3b	24 Nov.	15:00h	♂	2-3	2	≥ 16.5	93	78	18.0
A8	1 Dec.	11:30h	♀	≥ 3	1	12.8	74	90	17.4
B4	1 Dec.	15:05h	♂	opening	1	11.7	85	85	16.9
A11	2 Dec.	12:10h	♀	0.5	2	16.7	74	80	18.4
A2	2 Dec.	15:15h	♂	1-2	2	12.3	85	85	17.3

by Vaseline (this treatment was made with a male and a female flower). In a) gas exchange between tube and outside air was virtually unimpeded, in b) it was strongly retarded, and in c) it was blocked. The behaviour of the fly was observed during the first 15 min but later at hourly or longer intervals. To be effective, anaesthesia has to occur within some 10 min because flies normally remain only a few minutes inside the tube. To check the time required for asphyxia (experiment (9, d), a *L. porphyrina* was enclosed in a film canister of 30 cm^3, about a fourth of the tube's air space, and checked how long it took until it was dead.

RESULTS

Respiration and transpiration of different *Sapria* flowers

As expected, the respiration rate of *Sapria* flowers differed according to their age but to some extent also regarding their sex, time of the day and site factors (Table 1). The flowers opening or already open for one day or less had relatively high values, on average 18.5 ± 9.66 µmol CO_2/m^2sec, those already open for more than two days but not senescent had lower rates, on average 12.96 ± 4.77 µmol CO_2/m^2sec, i.e. a decrease of 28%. The pattern for transpiration was similar. The young flowers had relatively high rates, 87.0 ± 24.48 µmol H_2O/m^2sec, whereas the old flowers had an average transpiration rate of 72 ± 17.89 µmol H_2O/m^2sec, i.e. a decrease of 17%. These decreases and the ratio between transpiration and respiration, which was 4.7 in the young and 5.6 in the old flowers, indicate that, with age, respiration diminishes more than transpiration. This agrees with the fact that the senescent flower had a very low respiration and, to a lesser extent, also a low transpiration rate, probably because of the breakdown of the plant's metabolism (Table 1). As expected, the bud had the lowest gas exchange (Table 1). Interesting is the difference in the respiration and transpiration between the sexes, higher in females. The reason presumably is due to an unusual feature found in *S. himalayana*. As demonstrated in studies on the natural and manual pollination (Bänziger, 2004), the ovules are not yet mature at the time of anthesis. The development of the more than 10,000 ovules in the large ovary evidently produces higher respiration in females.

Respiration of different parts of *Sapria* flowers

The difference between the respiration rate of the whole flower minus that of all the lobes gives the respiration rate of the inner parts of the flower, the tube. From Table 2, the average of the respiration rate of the tube was calculated to be 13.9 µmol CO_2/m^2sec, that of the 10 lobes 2.6 µmol CO_2/m^2sec. The outer side of the 10 lobes and the external side of the tube with their hard and smooth surface are not considered in this analysis because, as shown in Table 1, the gas exchange of the outer parts of the bud, which has a similar surface structure, is relatively small. Thus, the main proportion of the respiration rate comes from the tube, viz. 84% although its surface is only 106 cm^2, whereas the 10 lobes contribute just 16% despite their larger surface of 164 cm^2 (surfaces measured in Material and Methods, and see Tables 1, 2). The transpiration rate has not been assessed because condensation of water occurred on the walls of the chamber in some cases. Nonetheless, this indicates that the relative humidity inside the flower as well as in the chamber was around 100%.

Respiration and water vapour release of the soil at the *Sapria* sites

On the slopes of different exposures with mixed evergreen forest on different dates and at a distance of <3 m from the *Sapria* flowers, the soil respiration was 1.8 ± 0.9 µmol CO_2/m^2sec; the release of water vapour was always <50 µmol H_2O/m^2sec.

CO_2 emanation from a dead rabbit

The CO_2 emanation from 111 cm^2 on the abdominal flank of a rabbit 12 hours, two, four, and six days after its death was 2.8, 2.4, 3.3, and 3.3 µmol CO_2/m^2sec, respectively. The overall average was 2.95 ± 0.44 µmol CO_2/m^2sec.

Table 2. Respiration rates of the tube compared to the lobes of flowers of ***Sapria himalayana***. The respiration of the lobes has been prevented by Vaseline (unless they had already been cut off to make space for the chamber). Acronyms in the first column refer to the cluster site and flower index of ***S. himalayana*** studied on Doi Suthep, N Thailand.

Site	Date	Time	Sex	Days since flower open	Treatment	Respiration $\mu molCO_2/m^2sec$	Ambient air temperature °C	Ambient air humidity RH%
B4	1 Dec.	15:05h 15:20h	♂	opening	1 lobe cut off Vaseline on both sides of 9 lobes Difference (9 lobes)	11.7 11.1 0.6	16.9 16.8	85
A11	2 Dec.	12:10h 12:55h	♀	0.5	2 lobes cut off Vaseline on both sides of 8 lobes Difference (8 lobes)	16.3 14.2 2.1	18.4 17.9	80
A2	2 Dec.	15:15h 15:44h	♂	1-2	2 lobes cut off Vaseline on both sides of 8 lobes Difference (8 lobes)	12.3 8.4 3.9	17.3 17.0	85

Table 3. Cooling of ***Sapria himalayana*** flowers during the dry season. Highest and lowest cooling of flower disk compared to ambient air is shown in the last column. *Time when the minimum or maximum of humidity or temperature were registered during the respective measuring session. Age: days since flower open. Acronyms in the first column refer to the cluster site and flower index of ***S. himalayana*** studied on Doi Suthep, N Thailand.

Site; Flower Sex; Date	Session time	Age	Relative Humidity (%) Time when min/ max occurred*				Temperature (°C) Time when min/ max occurred*				Disk cooler than ambient (°C)
			Ambient	Tube	Ambient	Tube	Ambient	Disk	Ambient	Disk	
H3, ♂	11:50–	1.5	12:05 h	12:05 h	13:05 h	13:05 h	12:05 h	12:05 h	13:05 h	13:05 h	-0.3°, -1.1°
22 March	17:30 h		59.0%	99.9%	56.2%	99.9%	23.5°C	23.2°C	24.0°C	22.9°C	
B10.3, ♂	07:00–	3	07:05 h	07:05 h	14:40 h	14:40 h	07:05 h	07:05 h	14:40 h	14:40 h	-1.2°, -2.9°
26 March	14:50 h		66.8%	99.9%	30.7%	99.9%	20.1°C	18.9°C	26.1°C	23.2°C	
B10.2, ♀	09:35–	1.5	09:35 h	09:35 h	14:50 h	14:50 h	09:35 h	09:35 h	14:50 h	14:50 h	-1.8°, -3.3°
27 March	15:05 h		58.2%	99.9%	30.7%	99.9%	23.9°C	22.1°C	26.1°C	22.8°C	
D5.1, ♂	14:50–	<1	15:15 h	15:15 h	19:35 h	19:35 h	15:15 h	15:15 h	19:35 h	19:35 h	-3.0°, -1.0°
4 April	19:35 h		31.7%	99.9%	60.2%	99.9%	26.3°C	23.3°C	22.4°C	21.4°C	
D5.2, ♀	15:35–	<1	15:50 h	15:50 h	20:10 h	20:10 h	15:50 h	15:50 h	20:10 h	20:10 h	-2.4°, -0.8°
5 April	20:30 h		44.0%	99.9%	63.3%	99.9%	25.4°C	23.0°C	22.2°C	21.4°C	
D5.3, ♂	10:45–	0.5	11:00 h	11:00 h	14:00 h	14:00 h	11:00 h	11:00 h	14:00 h	14:00 h	-2.0°, -3.3°
6 April	15:35 h		59.5%	99.9%	44.9%	99.9%	23.5°C	21.5°C	26.1°C	22.8°C	

Table 4. Thermogenesis in flowers of ***Sapria himalayana*** during the rainy season. Acronyms in the first column refer to the cluster site and flower index of ***S. himalayana*** studied on Doi Suthep, N Thailand.

Site, Flower Sex	Date; Time	Days since flower open	Relative Humidity %		Temperature °C		Disk warmer than ambient °C
			Ambient	In tube of flower	Ambient	Disk of flower	
RD3.1, ♀	27 Sept.; 17:10h	1	98.0	99.9	20.3°	22.1°	+1.8°
RA8.1, ♂	30 Sept.; 13:30h	1	99.9	99.9	20.8°	21.5°	+0.7°
RA5.1, ♂	2 Oct.; 12:25h	<1	95.6	99.9	22.1 °	24.3°	+2.2°
RD3.4, ♀	5 Oct.; 13:15h	1	99.9	99.9	21.0°	22.3°	+1.3°
RB9.1, ♂	8 Oct.; 16:50h	1	99.9	99.9	20.5°	21.5°	+1.0°
RA8.3, ♀	12 Oct.; 15:15h	2 1/2	99.9	99.9	20.1°	21.0°	+0.9°

Hence even under relatively warm conditions (22.9 to 28.9 °C), the CO_2 emanation from a 6-days-old cadaver of a rabbit was still relatively low and comparable to that of the soil at the *Sapria* sites.

Temperature and humidity in the *Sapria* flower during the dry and during the rainy season

As shown in Table 3, the inner parts of the flower, i.e. the disk and stalk, were consistently cooler than the ambient air, by –1.1 to –3.3°C early afternoon when the metabolism was most active, during the dry season. The relative humidity in flower tube was constantly near saturation, 99.9%, despite the ambient humidity was only 30.7% to 66.8% (average of minima 40%, of maxima 61%). Conversely (Table 4), during the rainy season the disk and stalk were consistently slightly warmer than the ambient air, by +0.7° to +2.2°C, and the humidity in the tube again 99.9%, and the ambient 95.6% to 99.9%.

Results of the laboratory measurements of *Sapria* flower dimensions

Male 1, 2. Weight of whole flower, 170 g, 176 g. Dry weight, 10 g, 12 g. Total tissue volume (without the empty inner tube space), 154 cm^3, 156 cm^3. Inner tube volume (empty space), 108 cm^3, 119 cm^3. Female 1, 2. Weight of whole flower, 192 g, 204 g. Dry weight, 15 g, 19 g. Total tissue volume (without the empty inner tube space), 171 cm^3, 198 cm^3. Inner tube volume (empty

space), 69 cm^3, 82 cm^3.

Because the surface areas are technically less exactly measurable, we took overall averages for all 10 lobes together, and similarly for the four tubes. Namely, total inner surface area of 10 lobes, 164 cm^2; inner surface area of tube, 106 cm^2.

Results of experiments with flies

The attractiveness of different baits was (experiments 6–9): (6) blowflies were seen flying onto and crawling below the leaf litter under which a dead, smelly rat or liver was concealed. (7) blowflies, mainly *C. defixa* (Walker), *C. villeneuvi* Patton, and *L. papuensis*, flew onto the netting and crawled all over it in attempts to find an entrance to the flower of *Ra. kerrii*. (6) and (7) indicate that these blowflies are capable to locate a food or oviposition site by olfaction alone. (8) a total of 52 blowflies, *L. porphyrina, L. papuensis, L. sinensis, C. pinguis* (Walker) and *C. megacephala* (Fabricius), settled on the netted boxes with meat or liver in comparable numbers, whereas no fly was seen approaching or settling on the box with the dry ice. This indicates that CO_2 from dry ice is not attractive to these blowflies.

No anaesthetic role by CO_2 was detected (9, a–c). All four flies flew off when trials were discontinued after 28 h 40 min, 24 h 45 min, 24 h 58 min, and 24 h 8 min, respectively. The CO_2 concentration inside the tube evidently never reached the anaesthesia-inducing level. Also, enough oxygen remained in the tube for the flies to survive for more than 24 h, even under gas exchange prevention. The fly needed little oxygen (9, d): asphyxia occurred some 20 hours after being enclosed in the film canister with only a fourth of the flower's air space inside the tube.

DISCUSSION

Respiration and transpiration

Our results showing a strong emanation of CO_2 by *S. himalayana* confirm the prediction of Patiño *et al*. (2002). However, their calculations predicted a ten times higher CO_2 concentration in *Ra. tuan-mudae* compared to our species. Namely, for the tube's interior they calculated a concentration approximately 76 times that of the air in the forest understory. In *S. himalayana*, our measured CO_2 concentration was only five to nine times the ambient's concentration. Although the CO_2 production in the three to four times larger flowers of *Ra. tuan-mudae* can be expected to be much higher than in *S. himalayana*, the concentrations should be comparable. We think that their theoretical calculations are likely to be overestimated.

Patiño *et al*. (2000, 2002) did not study the transpiration. The high transpiration rate we found inside the flower is important and requires an explanation. It is in connection with two unexpected features revealed in the present study. First, the humidity in the flower's tube was constantly near saturation, even during the dry season when the ambient humidity was as low as 31% (average of minima 40%). Second, the flower was constantly slightly thermogenic (+0.7° to +2.2°C, average of temperature increase +1.3°C) during the rainy season, but constantly cooler ('cryogenic') than the ambient (–1.1° to –3.3°C early afternoon, average of maximum cooling –2.1°C) during the dry season, respectively (Tables 3 and 4). ('Cryogenic' would be the appropriate term for this cooling effect because analogous to thermogenic; however, the term cryogenic is already preoccupied for processes at very low temperatures, e.g. below –100°C.) An ecophysiological explanation of the surprising finding of the cooling lies in the fact that the pollen must be in a fluid suspension, and the stigma wet, in order to be acquired and later deposited by the pollinator (Bänziger, 1996, 2004). This requires constant high humidity inside the tube and, when the outside air is dry, the flower needs to transpire at high rates, which causes cooling. Cooling was found also in *S. ram* Bänziger & Hansen and in *Ra. kerrii* Meijer (Bänziger, unpublished) though in the latter the cooling was relatively weak, evidently because its habitat (S Thailand) has a much less pronounced dry season. Patiño *et al*. (2000, 2002) found that *Rh. lowii* and *Ra. tuan-mudae* were only thermogenic – not surprising since they grew in perhumid habitat. Among the diverse functions proposed for thermogenesis (reviews in Seymour, 2010; Johnson and Schiestl, 2016) is an increased release of volatiles. Cooling would thus seem to be a drawback, albeit not a strong one with only –1° to –3°C in the otherwise hot climate. Conversely, it could be an advantage in retarding a too fast depletion of volatiles. At any rate, strong transpiration is likely to have a secondary advantage. A humid air plume in dry hot ambient is likely to be attractive to flies at close range. Flies are sensitive to water deprivation, e.g. *Musca domestica* L. loses 30% water in 6–8 h in dry air (Wiesmann, 1960). *Lucilia sericata* (Meigen) will oviposit only on moist substrates (Barton Browne, 1962, 1979; Barton Browne and Rogoff, 1959; Cragg and Ramage, 1945). High humidity inside the flowers of *Asarum caudatum* Lindl. (Aristolochiaceae) has also been suggested by Vogel (1978) as one of the attractants of Mycetophilidae and other flies. With 170–204 g fresh weight but only 10–19 g dry weight, the flower of *S. himalayana* stores some 150 to nearly 200 ml of water in its spongy tissue. Depletion of water can be readily replenished thanks to the hosts' (*Tetrastigma* spp.) efficient water flow – as evidenced by jungle trekkers' abuse to cut sections of the stem to drink the water dripping out of the lower end. We found no reference about flowers continuously producing high humidity with consequent cooling when in dry environment, hence this physiological feature in *Sapria*'s reproduction strategy appears to be a novel finding.

The role of volatiles

The pollination syndrome in Rafflesiaceae is sapromyiophily (*sensu* Van der Pijl, 1960). It is based on a fraud where flowers mimic, without actually offering, a decomposing food or oviposition substrate for flies. (Bänziger (1991) proposed non-deception, but Bänziger (1995, p 356) reinterpreted it as deception.) Our result that 80% of the respiration and transpiration occurs in the tube is important for pollination. Except for the aperture, the tube encloses completely the reproductive organs. This also reduces too fast dissipation of volatiles, without precluding a degree of ambient air diffusion into the tube with its vital oxigen. Experiments (6) and (7) demonstrate that cadaveric volatiles are evidently pre-eminent in attracting the sylvatic flies of our habitats, since visualization is not required to find the flower, though it likely allows faster locating of the resource. Beaman *et al*. (1988) found visual attraction important though subordinate to putrid odours in blowflies on *Ra. pricei* Meijer, but their experimental set-up was different from ours.

Putrid volatiles have been analyzed by head space method in *Ra. tuan-mudae* by Patiño *et al*. (2002). They found dimethyl disulphide and dimethyl trisulphide (Patiño, Edwards and Grace, unpublished). These volatiles were also present in *S. himalayana* and *S. ram* (Kaiser and Bänziger, unpublished). Interestingly, when sniffing inside *Ra. kerrii*, a pleasant 'fruity' scent was perceived instead of the malevolent smell just outside the flower (Bänziger, 1991). Indeed, subsequent analyses detected, among else, limonen, linalool und eucalyptol (Kaiser and Bänziger, unpublished), all variously fragrant. An explanation for this apparently contradicting finding is that the olfactory receptor neurons in human noses temporarily shut down receptivity (anosmy) to those particular volatiles – the smelly amines in *Ra. kerrii* – when they are very strong. Interestingly, Norhazlini *et al*. (2020) also found a volatile with fruity fragrance in *Ra. kerrii*, 1,2-benzenedicarboxylic acid diethyl ester. *Rhizanthes* does not smell cadaveric (Bänziger, 1995). In *Rh. lowii* acetoin, ethylhexanol, diethyltoluamide were found (Patiño, Edwards and Grace, unpublished) whereas in *Rh. infanticida* limonene, nonanal, decanal, acetic, butyric, caproic and caprylic acids were present (Kaiser and Bänziger, unpublished). These scents are present in human and mammal body odours. The blowfly *L. porphyrina* was not only seen laying into the fur of dead mice and rats but occasionally also of live ones (hence not emanating putrid volatiles) caught uninjured in wide-meshed traps (Bänziger, unpublished).

The comparative importance of volatiles and CO_2 for pollinators

The attractive power of putrid odours to blowflies is well-known but has CO_2 any role in this? Patiño *et al*. (2000, 2002) proposed that high CO_2 emanation may increase the flowers' attractiveness, at least when combined with fetid volatiles. They listed many cases of insect attraction by CO_2. They also suggested that CO_2 may have an anaesthetic effect on the flies. They observed blowflies remaining inside *Ra. tuan-mudae* for very long times. We (H.B.) confirm this with similar observations on other Rafflesiaceae but interpret it as a normal resting behaviour which can be seen in blowflies when settled on leaves or twigs in the same habitat. Our experiments (9) show that there is no anaesthetic effect by CO_2 on flies inside *S. himalayana*. The CO_2 concentration evidently is much too low and the O_2 sufficient for the flies' low activity inside the tube with 69–119 cm^3 breathing space. We expect the same for *Ra. tuan-mudae*, even if one would consider its calculated (Patiño *et al*., 2002) 10-times stronger CO_2 concentration compared to *Sapria*. *Ra. tuan-mudae*'s flower's aperture of 15–18 cm diameter (Nais, 2001) allows fair gas exchange, additionally increased by air turbulence when flies fly into, within it, and out of it. In *S. himalayana* the aperture is only 1.8–3.7 cm, and flies do not fly but crawl into it (Fig. 2). As to the attractiveness of CO_2, our experiment (8) indicates that CO_2 alone is not effective in attracting the sylvatic blowfly species present in the habitat.

However, could not a blend of various fetid volatiles with CO_2 act synergistically as proposed by Patiño *et al*. (2000, 2002)? In the large body of literature on blowflies we found just one study indicating synergistic attraction. However, it was in a two compound combination (CO_2 bubbling through ethyl mercaptan) and its attractiveness for *L. sericata* was inferior to the combination where CO_2 was replaced by hydrogen sulphide or dimethyldisulphide (Cragg and Thurston, 1949). Doubtful effectiveness of a CO_2 synergistic action is also indicated by Swormlure, an artificial blend of compounds concocted to imitate those present in rotting meat (Coppedge *et al*., 1977). Despite the lack of CO_2 in Swormlure, it was just as attractive to blowfly *Cochliomyia hominivorax* (Coquerel) or even more attractive to *L. sericata* than fetid liver (Hall *et al*., 1995) which produces CO_2. Finally, one would expect our flowers to mimic as close as possible the smell of a cadaver. The CO_2 emanation of a dead rabbit was found to be lower or comparable to the CO_2 production of the forest soil. Hence the 5–9 times higher CO_2 emanation of *Sapria* bears no similarity to a cadaver. Such a surplus begs an explanation other than fly attraction (see below).

Unfortunately, the mentioned large body of literature treats mainly veterinary, medically and forensically important fly species. These are more or less strongly synanthropic but our species are sylvatic. Furthermore, blowflies exhibit appreciable behavioural differences even in closely related taxa. It is also important to distinguish between attractants and oviposition stimulants (e.g. Cragg, 1950). Hence caution is required when comparing our sylvatic species with experimental blowflies. To sum up, we are not in a position to prove or

exclude completely a synergistic role by CO_2, but we think that if it does have such a property, it is likely to be a minor one compared to cadaveric volatiles.

The strong emanation of CO_2 in our flowers may well be primarily a waste resulting from the synthesis of the many cadaveric volatiles in the flowers. According to Vogel (1962, 1993) the synthesis of such volatiles requires high energy input. Nevertheless, the resulting elevated CO_2 emanation may have some subsidiary function. Besides a possible minor synergistic attraction, CO_2 may reduce too rapid dissipation of volatiles. CO_2 is 1.5 times heavier than air and could somewhat keep down volatiles and humid air which are lighter than dry air. On the other hand, the strong production of water vapour in dry environmental conditions is a necessity for the proper functioning of the peculiar pollen presentation, acquisition, transportation and deposition in Rafflesiaceae (as described above, and see Fig. 2).

ACKNOWLEDGMENTS

H.B. thanks R. Kaiser for his laboratory analyses of the various scents collected by H.B.; he is indebted to (the late) S. Patiño for her expert guidance to the clusters of her study *Rhizanthes* in Brunei, and to P. Sukumalanand for his constant support for the decades-long research. Two anonymous reviewers improved the original manuscript. The National Parks, Wildlife and Plant Conservation Department, and the National Research Council of Thailand, extended permission (to H.B.) to carry out research in protected areas. A.G. thanks the Institute of Integrative Biology, Swiss Federal Institute of Technology (ETH), Zurich, for allowing the use of the delicate LCpro + Portable Photosynthesis System for our measurements.

LITERATURE CITED

Balete, D. S., P. B. Pelser, D. L. Nickrent, and J. F. Barcelona. 2010. *Rafflesia verrucosa* (Rafflesiaceae), a new species of small-flowered *Rafflesia* from eastern Mindanao, Philippines. Phytotaxa **10(1)**: 49–57.

Bänziger, H. 1991. Stench and fragrance: unique pollination lure of Thailand's largest flower, *Rafflesia kerrii* Meijer. Nat. Hist. Bull. Siam Soc. **39**: 19–52.

Bänziger, H. 1995. Ecological, morphological and taxonomic studies on Thailand's fifth species of Rafflesiaceae: *Rhizanthes zippelii* (Blume) Spach (Rafflesiaceae). Nat. Hist. Bull. Siam Soc. **43**: 337–365.

Bänziger, H. 1996. Pollination of a flowering oddity: *Rhizanthes zippelii* (Blume) Spach (Rafflesiaceae). Nat. Hist. Bull. Siam Soc. **44**: 113–142.

Bänziger, H. 2004. Studies on hitherto unknown fruits and seeds of some Rafflesiaceae, and a method to manually pollinate their flowers for research and conservation. Linzer biol. Beitr. **36**: 1175–1198.

Bänziger, H. and B. Hansen. 1997. Unmasking the real identity of *Sapria poilanei* Gagnep. emend., and description of *S. ram* sp. n. (Rafflesiaceae). Nat. Hist. Bull. Siam Soc. **45**: 149–170.

Bänziger, H. and B. Hansen. 2000. A new taxonomic revision of a deceptive flower, *Rhizanthes* Dumortier (Rafflesiaceae). Nat. Hist. Bull. Siam Soc. **48**: 117–143.

Bänziger, H. and T. Pape. 2004. Flowers, faeces and cadavers: natural feeding and laying habits of flesh flies in Thailand (Diptera: Sarcophagidae, *Sarcophaga* spp.). J. Nat. Hist. **38(13)**: 1677–1694.

Bänziger, H., A. Lamb and A. Kocyan. 2007. Bisexual *Rhizanthes lowii* (Beccari) Harms (Rafflesiaceae) from Borneo: first description of flowers, fruits and seeds. Nat. Hist. Bull. Siam Soc. **55**: 341–352.

Barkman, T.J., S.-H. Lim, K. Mat Salleh and J. Nais. 2004. Mitochondrial DNA sequences reveal the photosynthetic relatives of *Rafflesia*, the world's largest flower. Proc. Natl. Acad. Sci. USA **101(3)**: 787–792.

Barkman, T.J., M. Bendiksby, S.-H. Lim, K. Mat Salleh, J. Nais, D. Madulid and T. Schumacher. 2008. Accellerated rates of floral evolution at the upper size limit for flowers. Current Biology **18(19)**: 1508–1513.

Barton Browne, L. 1958. The choice of communal oviposition sites by the Australian sheep blowfly, *Lucilia cuprina*. Aust. J. Zool. **6(3)**: 241–247.

Barton Browne, L. 1962. The relationship between oviposition in the blowfly *Lucilia cuprina* and the presence of water. J. Insect Physiol. **8(4)**: 383–390.

Barton Browne, L. 1979. The behavior and nutritional requirements of adults of *Lucilia cuprina* – possibilities for modification. National Symposium on the Sheep Blowfly and Fly Strike in Sheep. Pp 45–57. Dept. Agric. N. S. W. in conjunction with the Australian Wool Corporation, Sidney.

Barton Browne, L. and W.M. Rogoff. 1959. The "sheep factor" and oviposition in *Lucilia cuprina*. Aust. J. Sci. **21**: 189–190.

Beaman, R.S., P.J. Decker and J.H. Beaman. 1988. Pollination of *Rafflesia* (Rafflesiaceae). Amer. J. Bot. **75(8)**: 1148–1162.

Bendiksby, M., T. Schumacher, G. Gussarova, J. Nais, K. Mat-Salleh, N. Sofiyanti, D. Madulid, S.A. Smith and T. Barkman. 2010. Elucidating the evolutionary history of the Southeast Asian, holoparasitic, giant-flowered Rafflesiaceae: Pliocene vicariance, morphological convergence and character displacement. Molec. Phylog. and Evol. **57(2)**: 620–633.

Blarer, A., D.L. Nickrent, H. Bänziger, P.K. Endress and Y.-L. Qiu. 2000. Phylogenetic relationship of Rafflesiales based on two nuclear and four mitochondrial genes. Poster presentation. Amer. J. Bot. **87**: 171.

Bouman, F. and W. Meijer. 1994. Comparative structure of ovules and seeds in Rafflesiaceae. Pl. Syst. Evol. **193(1-4)**: 187–212.

Coppedge, J.R., E. Ahrens, J.L. Goodenough, F.S. Guillot and J.W. Snow. 1977. Field comparison of liver and a new chemical mixture as attractants for the screwworm fly. Environm. Entomol. **6(1)**: 66–68.

Cragg, J.B. and G.R. Ramage. 1945. Chemotropic studies on the blow-flies *Lucilia sericata* (Mg.) and *Lucilia caesar* (L.). Parasitol. **36(3-4)**: 168–175.

Cragg, J.B. and B.A. Thurston. 1949. The reactions of blowflies to organic sulphur compounds and other materials used in traps. Parasitol. **40(1-2)**: 187–194.

Davis, C.C., P.K. Endress and D.A. Baum. 2008. The evolution of floral gigantism. Curr. Opin. Plant Biol. **11(1)**: 49–57.

Elliott, S. 1990. The distribution, status and ecology of *Sapria himalayana* Griff. (Rafflesiaceae). Brit. Ecol. Soc. Bull. **11**: 246–249.

Hall, M.J.R., R. Farkas, F. Kelemen, M.J. Hosier and J.M. El-Khoga. 1995. Orientation of agents of wound myiasis to hosts and artificial stimuli in Hungary. Med. Vet. Entomol. **9(1)**: 77–84.

Heide-Jørgensen, H.S. 2008. Parasitic Flowering Plants. Brill, Leiden.

Hidayati, S.N., W. Meijer and J.L Walck. 2000. A contribution to the life history of the rare Indonesian holoparasite *Rafflesia patma* (Rafflesiaceae). Biotropica **32(3)**: 408–414.

Johnson, S.D. and F.P. Schiestl. 2016. Floral Mimicry. Oxford University Press.

Meijer, W. 1997. Rafflesiaceae. Flora Malesiana I, Vol. **13**: 1–42.

Nais, J. 2001. *Rafflesia* of the World. Sabah Parks and Natural History Publications (Borneo), Kota Kinabalu, Malaysia.

Nickrent, D.L., A. Blarer, Y.-L. Qiu, R.Vidal-Russell and F.E. Anderson. 2004. Phylogenetic inference in Rafflesiales: the influence of rate heterogeneity and horizontal gene transfer. BMC Evol. Biol. **4(1)**: 40.

Nikolov, L.A., P.K. Endress, M. Sugumaran, S. Sasirat, S. Vessabutr, M. Kramer and C.C. Davis. 2013. Developmental origins of the world's largest flowers, Rafflesiaceae. Proc. Natl. Acad. Sci. USA **110(46)**: 18578–18583.

Nikolov, L.A., Y.M. Staedler, S. Manickam, J. Schönenberger, P.K. Endress, E.M. Kramer and C.C. Davis. 2014. Floral structure and development in Rafflesiaceae with emphasis on their exceptional gynoecia. Amer. J. Bot. **101(2)**: 225–243.

Norhazlini, M.Z., J. Mailina, M. Shalini, M.A. Nor Azah and H. Zulhazman. 2020. Assessing the floral volatile constituents of male and female *Rafflesia kerri* (sic) Meijer from Lojing Highlands, Peninsular Malaysia. IOP Conf. Series: Earth and Environmental Science **549(1)**: 012068.

Patiño, S., J. Grace and H. Bänziger. 2000. Endothermy of flowers of *Rhizanthes lowii* (Rafflesiaceae). Oecologia **124(2)**: 149–155.

Patiño, S., T. Aalto, A.A. Edwards and J. Grace. 2002. Is *Rafflesia* an endothermic flower? New Phytologist **154(2)**: 429–437.

Seymour, R. 2010. Scaling of heat production by thermogenic flowers: limits to floral size and maximum rate of respiration. Plant, Cell and Environment **33(9)**: 1474–1485.

Takhtajan, A. 1997. Diversity and classification of flowering plants. Columbia University Press, New York.

Tanaka, N., H. Nagamasu, S. Tagane, M.M. Aung, A.K. Win and P.P. Hnin. 2019. Contributions to the flora of Myanmar IV: A new species and a newly recorded taxon of the genus *Sapria* (Rafflesiaceae). Taiwania **64(4)**: 357–362.

Trias-Blasi, A., J.A.N. Parnell, P. Pornpongrungrueng and P. Kochaiphat. 2020. Vitaceae. Flora of Thailand **14**, 4: 588–669.

Van der Pijl, L. 1960. Ecological aspects of flower evolution. II. Zoophilous flower classes. Evolution **15(1)**: 44–56.

Vogel, S. 1962. Duftdrüsen im Dienste der Bestäubung. Über Bau und Funktion der Osmophoren. Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, Nr. 10. Akademie der Wissenschaften und der Literatur, Mainz. 165 pp.

Vogel, S. 1978. Pilzmückenblumen als Pilzmimeten. Flora **167(3-4)**: 329–366.

Vogel, S. 1993. Betrug bei Pflanzen: Die Täuschblumen. Abhandl. Mathematisch-Naturwiss. Klasse, Jg. 1993, Nr. 1.

Wiesmann, R. 1960. Untersuchungen über die Sinnesfunktionen der Antennen von *Musca domestica* L. im Zusammenhang mit dem Köderproblem. Mitt. Schweiz. Entomol. Ges. **33**: 121–154.