

## STENCH AND FRAGRANCE: UNIQUE POLLINATION LURE OF THAILAND'S LARGEST FLOWER, *RAFFLESIA KERRII* MEIJER

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### ABSTRACT

Rare *Rafflesia kerrii* is described for the first time from blooming male and female flowers. Females can be distinguished from males by the presence of an obliquely set band along the lower rim of the disk. *R. kerrii*'s distribution is extended farther south and north than hitherto reported, to Perak (W. Malaysia) and Prachuab Khirikhan (S. Thailand) where 12 colonies with 60 buds were found in an area ca. 2 km<sup>2</sup> at 500–850 m a.s.l. The habitat was unusually rich in *Tetrastigma* (Vitaceae) lianas though only *T. quadrangulum* Craib et Gagnep. is confirmed as host among 10 spp. present. A strong smell of carrion is emitted from rafflesia's perigone lobes, while a weaker fruity fragrance—unknown in other rafflesias—is produced in the tube's cavity, the scents being kept separate by the diaphragm. Carrion flies *Chrysomya villeneuvei* Patton, *C. rufifacies* (Macquart), *Lucilia porphyrina* (Walker) and *Hypopygiopsis tumrasvini* Kurahashi (Calliphoridae) are attracted by the stench and the 'festerling sore' appearance (lurid colour, crater shape, white blotches and/or whitish mold on processes) of the flower. The functions of the fragrance (e.g. to advertise carbohydrates, essential to adult flies) is discussed together with the physiology of the flies. Surplus pollen mush which has dropped from the anthers and a slimy secretion coating the parts below the disk can be sucked by the flies. They climb channels leading to the anthers, which are positioned in such a way that pollen cannot be stolen but only smeared onto the back of the flies' thorax. In the female flower the process is similar, the pollen clot being rubbed off onto the stigmatic surface set between the oblique band and the column. It is proposed that *R. kerrii* is not a deceptive flower and that the flies might act as long distance pollinators between rafflesias flowering up to several weeks apart. The relatively modest size of infected hosts indicates that rafflesias may be able to survive parent host death and spread their population by vegetative infection of the host's lateral runners.

### INTRODUCTION

Rafflesias have baffled scientists since early in the last century when reports from Sumatra about *Rafflesia arnoldii* R. Br., the first of some 14 spp. of the genus (MEIJER, 1984; MAT SALLEH & LATIFF, 1989), caused a sensation in the botanical world. The flowers' phenomenal size, ephemeral blooming, unlikely parasitic existence, vivid colours, and lack of chlorophyll, leaves, stem and roots make them a living paradox. Because of their rarity and concealed existence as filaments within the host liana (*Tetrastigma* spp.) for much of the time, their biology remains largely unknown. Seed dispersal and infection of the roots of a new host are an enigma, but possibly the most disconcerting aspect of these 'flowering beauties' is their bouquet: a cadaveric stench of rotting snakes. The concomitant buzzing of blowflies, well-known pests associated with excrement, festering sores

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and carrion, around the flowers dispels any lingering doubt about the provenance of the stench. Yet, in a new surprise revealed in this study, from the very heart of some rafflesias a sweet fragrance emanates.

The genus occurs mainly within the W. and S. Malesian floristic region, with Thailand the only country outside Malesia so far with a rafflesia (*sensu stricto*), *R. kerrii* Meijer. *R. kerrii* has been reported mainly from 5 localities in Ranong and Surat Thani Provinces (MEIJER, 1984; NIYOMDHAM & KUBAT, 1987; MEIJER & ELLIOTT, 1991). The known southernmost limit extends somewhat south of the Kangar-Pattani line, the boundary of the Malesian flora on the Malay Peninsula (WHITMORE, 1975), with a collection from a site on Bukit Tepoh which marks the border area of Narathiwat Province of Thailand with Kelantan State, Malaysia (MEIJER & ELLIOTT, 1991).

The present study extends the rafflesia's distribution significantly farther north, to Prachuab Khirikhan, not contiguous with other known populations. Buds acquired by the author in Upper Perak also extend its presence farther south into Malaysia but, as mentioned in Appendix 2, the buds' origin is not certain. In the absence of precise data from Malaysia, *R. kerrii* can still be considered a Thai endemic, but it is virtually certain that the species' distribution reaches into northern W. Malaysia and also S. Burma. Kerr's collection near Ban Lam Lieng (Ranong Prov.) is only 10 km from the Burmese border (Tenasserim Division), and new findings reported here put it even nearer to Burma.

If rafflesias are considered in the broad sense, then Thailand is home to at least two more species: *Sapria himalayana* Griff. in northwest and west Thailand (HOSSEUS, 1907; HANSEN, 1972; SMITINAND, 1980; BÄNZIGER, 1988; ELLIOTT, in prep.); and *S. poilanei* Gagnep. in the southeast (SMITINAND, 1980).

With an expansion reaching 0.7 m, *R. kerrii* is not quite as large as *R. arnoldii*'s flower of close to 1 m, but it is still the largest flower of Thailand. Yet only as recently as 1984 has it become known to science with a valid description by MEIJER. Botanists had actually sporadically collected it since 1927 but it was 'forgotten' until SMITINAND (1980) mentioned it in a list of Thai plants under the name *R. patma* B1. (initially identified by Kerr), a species known only from Sumatra and Java. Furthermore, no one seems to have acknowledged that from time immemorial local forest dwellers, ethnic Thais and other peoples of the Malay Peninsula, have known and used it. As *dok bua tuum* and *bua phut* (Thai: ดอกบัวตูม in Ranong Prov. and บัวผุด in Surat Thani Prov., respectively) and *bunga patma* (*pakma*) (Malay, applied also to other rafflesias), it has been ascribed medicinal properties. Possibly because of the rarity of blooming flowers it is believed to possess magical and mystic-religious powers, to confer invulnerability and assist in attaining Nirvana (pers. comm. by a gum tapper of Ranong).

In the most detailed study of *R. kerrii* so far, MEIJER & ELLIOTT (1991) summarized previous information and added new taxonomic and ecological data obtained from freshly cut buds. Fruits and seeds remain unknown.

*R. kerrii* was unexpectedly found by the author while investigating the interrelationship between rare moths and lianas (e.g. BÄNZIGER, 1989). Fly activity on a blooming flower prompted an investigation of the pollination mechanism, as a comparison for an ongoing similar project on dipteran pollination of orchids. Additional details not directly connected with pollination ecology are also included in the present research — the first of blooming flowers and living bud colonies of *R. kerrii* in the wild.

At the time of my research I was not aware of the excellent study of the pollination mechanism of *R. pricei* Meijer by BEAMAN et al. (1988) in which for the first time the details of rafflesia pollination are described. While the pollen transfer mechanism is the same in the two rafflesias, there appear to be appreciable differences in the way the two rafflesias 'manipulate' fly behaviour for their own ends. This will be discussed in a later paper.

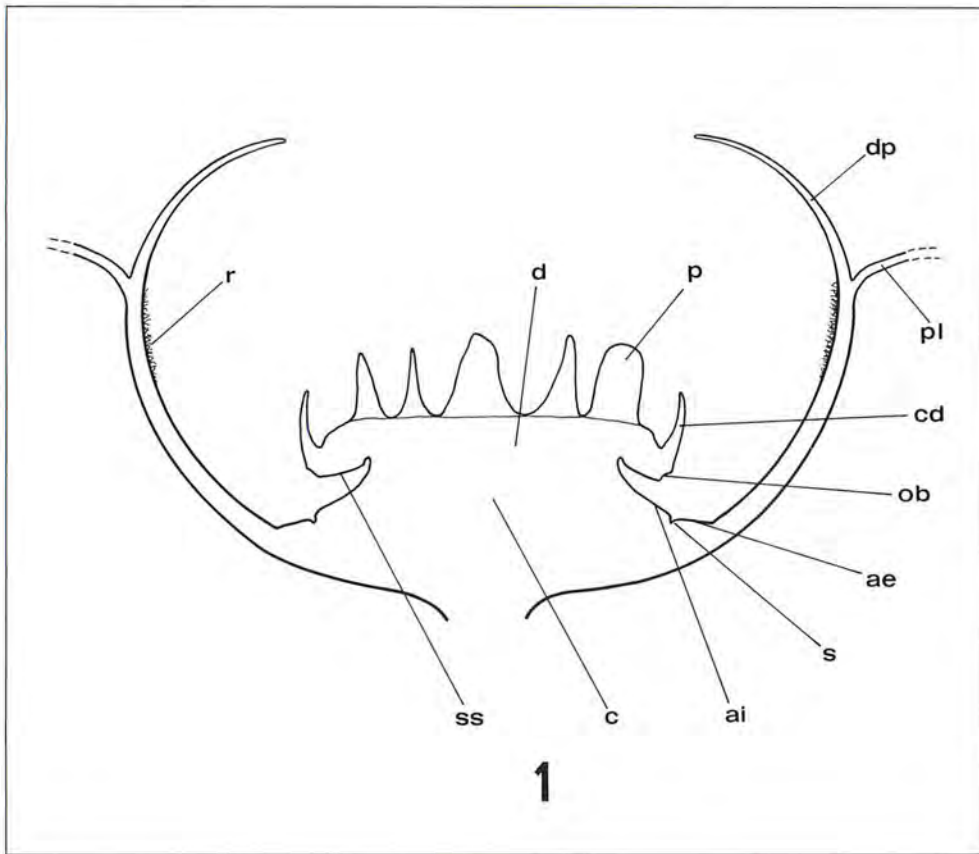
## H A B I T A T

In contrast to MEIJER & ELLIOTT (1991) I carried out my research alone without telling locals what I was studying. Furthermore, in order to protect this rare rafflesia from unscrupulous collectors and visitors, I have chosen not to reveal the exact location of the plants at this stage. The site is some 300 km north of what heretofore was the most northerly population known. A 3-hour ascent from the nearest road leads one to the main colonies at 700–750 m. The climb is through notoriously tricky forest (confirmed by local people)—despite marks left on my way, I am not sure if I ever managed to follow the same track twice.

The rafflesias grew on the southeast-facing river catchment, on slopes of up to about 30° inclination, between 475 and 840 m. At elevations lower than ca. 300 m and higher than 900 m the vegetation was rather xeric and darker, respectively, less suitable for host *Tetrastigma* spp. I did not find any *R. kerrii* on the northwest-facing slopes above the same stream, where lianas were scarce in general. Unlike some other rafflesia species (e.g. MAT SALLEH & LATIFF, 1989), *R. kerrii* was not close to streams, the nearest being some 50 m away. Big granitic boulders and smaller rocks were frequent but mostly not adjacent to the rafflesias. The forest (Fig. 3) was evergreen and the vegetation remained green even during the exceptionally arid dry season of 1991 when no rain fell from December until April. Fire does not seem to reach the sites normally though it rages through more peripheral, drier sections of the mountain. Leaf litter covered the soil completely. Small trees predominated, interspersed with unusually abundant lianas but few large trees. The canopy allowed some rays to reach the ground and the blooming rafflesias of colonies 3 and 4 possibly received direct sunlight some 5–10% of the day. The ground flora was quite sparse, mainly ferns and seedlings; no Gramineae were seen at the study sites. Many rattans and other spiny plants made passage arduous.

Plants in the vicinity of colony No. 4 included, besides unusually common *Tetrastigma* spp., several Menispermaceae (*Stephania reticulata* Forman, *Cyclea atjehensis* Forman, *Diplocisia glaucescens* (Bl.) Diels), *Cissus* sp., *Cycas circinalis* L., *Justicia valida* Ridl. and a number of unidentified herbs.

Relevant vertebrates observed were squirrels such as the common *Callosciurus flavimanus* G. S. Hillaire, *C. caniceps* (Gray) and the mouse deer (*Tragulus javanicus* (Osbeck)). They may play a role as seed dispersers of rafflesias. Gibbons (*Hylobates lar* L.), leaf monkeys (*Presbytis* sp.) and macaques (*Macaca nemestrina* (L.) or *M. arctoides* (Geoffroy)) were seen or heard on most days; head, skin, intestines of macaques and leaf monkeys were occasionally found at hunters' camps. They were covered with egg-laying and feeding blowflies, rafflesias' pollinators. These mammals may also contribute to seed dispersal of *Tetrastigma* spp.



Figures 1–2. Cross section of blooming flower of *R. kerrii*, showing main morphological characteristics. 1, Female; 2, Male (part). a = anther; ae = annulus exterior; ai = annulus interior; c = column; cd = collar of disk; d = disk; dp = diaphragm; ob = oblique band; p = process; pl = perigone lobe; r = ramentae; s = sulcus; ss = stigmatic surface.

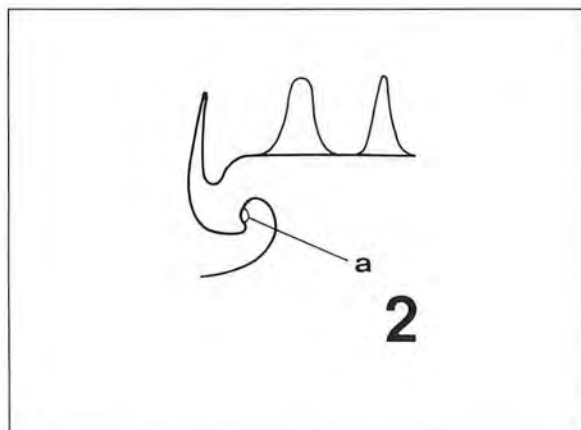




Figure 3. Habitat of *R. kerrii*. A female flower can be seen near the bottom centre. The two arrows point to the stem of the host, the liana *Tetrastigma quadrangulum*.





Figure 4. Male *R. kerrii*, 0.5 m across, in full bloom. Two blowflies have settled on the right perigone lobe, and two are in flight above the diaphragm on the left.



Figure 5. Female *R. kerrii* just past full bloom, the distal parts of the perigone lobes already wilting. No blowflies present.

## STUDY POPULATION

The study area was visited 11 times during 4 periods: 26–27 January, 12 February, 5–8 March, 7–10 April 1991. Host assessment was not always successful as the digging had to be carried out with great care or avoided altogether in order to minimize damage; the roots sometimes extended deep down or between rocks.

## Colony cluster A:

At 475 m, 3–4 km (1.5 h walk) from base. Colony No. 7 with 1 dead bud of 12 cm across and 2 larger buds or flowers in very advanced stage of decay, 30 cm from each other. Host almost certain *T. quadrangulum* of 6 x 8 cm stem size. Colony No. 8, 15 m further on, with 2 healthy buds of 8 and 14 cm, in close contact. Host *T. quadrangulum* ascertained by following the root to the liana stem of 4 x 5 cm (Bänziger coll. No. 901).

## Colony cluster B:

At 500 m, ca. 250 m further on from A. Colony No. 1 with 13 dead buds up to 10 cm, a moribund and a healthy one of 14 cm, over an area of 5 x 6 m. Host almost certain 1–3 *T. quadrangulum* of 4 x 5 cm stem size. A very small *Tetrastigma* sp. 1 was present further away. Roots with most buds decaying, hence high bud mortality. Colonies No. 10, 11, 12, at 30, 50 and 80 m from No. 1, respectively; with 5, 5 and 4 buds, respectively, dead or rotten; about medium size and some 0.5 m from each other. Host almost certain *T. quadrangulum*, the largest 5 x 6 cm in stem size.

## Colony cluster C:

Possibly some 2 km (ca. 1.5 h walk) further up from B. Colony No. 3 at 720 m, with a rotten and a healthy bud of 17 cm which developed into flower No. 2 (Figs. 3, 5). Host was *T. quadrangulum*, ascertained by digging and following the root to the liana stem of 2 x 3 cm (Bänziger coll. No. 896). *T. papillosum* and *T. sp. 1* were also present nearby. Colony No. 4, at 750 m, ca. 200 m further up from No. 3, with 2 small buds of 7 cm, 2 larger ones of 19 cm (Fig. 11), one of which became flower No. 3 (Fig. 19), and the blooming flower No. 1 (Fig. 4), and 3 long since rotten flowers. Area just 1 x 1.5 m, some buds in close contact. Host was *T. quadrangulum* ascertained by digging and following the root to the liana stem of 3 x 5 cm which bore fruits (Bänziger coll. No. 864, 876). *T. papillosum* and *T. sp. 1* were also growing nearby. Colony No. 9, at 765 m, ca. 70 m further up from No. 4, with 2 buds of 4.5 and 9 cm and 4 dead ones, about 0.5 m from each other. Host probably *T. quadrangulum* but *T. sp. 1* and *T. sp. 11* were also nearby.

Location of colonies No. 2, 5, 6 not certain as I lost my track. No. 2, at 710 m, with 2 aborted and 2 healthy buds of 10 (Fig. 10) and 12 cm, over an area of 2 x 3 m. Host possibly *T. sp. 1* but *T. quadrangulum* was present further away. No. 5, at 780 m, with 2 open, long since withered flowers. Host possibly *T. sp. 1* but *T. quadrangulum* was not far off. No. 6, at 840 m, with 4 aborted buds. Host unknown.

The roots infested were about 1.5–2 cm in width (Fig. 20). The parasitized lianas were nearly all of modest size, usually 3 x 5 cm across, but one was 6x8 cm. The basal 2–5 cm of buds and flowers were embedded in the soil and were about one to several m from where the stem of the host emerged from the ground. Because of their brownish colour, buds did not stand out much against the background of leaf litter, the young ones being completely submerged in it. Even the reddish, blooming flowers which lack the large white spots of other *rafflesia* species, were not too conspicuous against dead leaves. In one instance I was alerted by the stench of the flower before seeing it. Most conspicuous were dead buds and flowers due to their charcoal-like aspect.

With a maximum of some 15 buds (possibly growing on more than one host), colonies of *R. kerrii* are smaller than those of *S. himalayana* in which more than 100 buds sometimes emerge from a single host during the course of a flowering season (ELLIOTT, pers. comm. and pers. obs.). However, the latter is a much smaller species and its main host rather large.

## OBSERVATIONS

### Hosts

Very little attention has been given to host plants in studies of *rafflesia* although they are of paramount importance to their conservation.

The hosts of *rafflesia* are restricted to *Tetrastigma* spp. (Vitaceae). BROWN's (1821) record of *R. arnoldii* on *Cissus* sp. appears to be a misidentification (LATIFF, 1984). In that taxonomic study 12 spp. occurring in (probably the Malaysian part of) the Malay peninsula are revised; the total number given for Malesia is 57 spp. GAGNEPAIN (1912, 1930) lists 39 spp. for Indochina and CRAIB (1926) 16 for Thailand.

At least 7 and probably as many as 10 species of *Tetrastigma* were found in my study area (coll. deposited at the Dept. Entomology, Faculty of Agriculture, Chiang Mai University (DEFACU)):

<i>T. cruciatum</i> Craib et Gagnep.	coll. No. 877, 892, 931, 936
<i>T. lanceolarium</i> Planch.	coll. No. 898, 929, 930, 942, 943
<i>T. papillosum</i> (Bl.) Planch.	coll. No. 890, 895, 944
<i>T. quadrangulum</i> Gagnep. et Craib	coll. No. 864, 894, 896, 900-902, 913
<i>Tetrastigma</i> sp. 1	coll. No. 876, 888, 889, 891, 893, 897, 899, 938, 939
<i>Tetrastigma</i> sp. 6	coll. No. 937
<i>Tetrastigma</i> sp. 7 (aff. <i>siamense</i> Gagnep. et Craib)	coll. No. 927, 928
<i>Tetrastigma</i> sp. 8	coll. No. 940
<i>Tetrastigma</i> sp. 10	coll. No. 933
<i>Tetrastigma</i> sp. 11 (aff. <i>garrettii</i> Gagnep.)	coll. No. 934, 935)

This is about 5/6 of the species found in the whole of West Malaysia and also of Doi Suthep–Pui National Park, well-known for its high biodiversity (BÄNZIGER, 1988; ELLIOTT et al., 1989), where about 12 species have been recorded (MAXWELL, pers. comm.). This mountain has been surveyed for close to a century and is, with 261 km<sup>2</sup>, much wider



than the area of *R. kerrii* of a few km<sup>2</sup> which I have visited 11 times. Two and even three species of *Tetrastigma* were in the close vicinity of some *R. kerrii* colonies. However, in my study area only *T. quadrangulum* (Fig. 3, 12), a new host, has been confirmed to be parasitized by *R. kerrii* though *Tetrastigma* sp. 1 is a candidate. Previously reported hosts of *R. kerrii* are *T. lanceolarium* (MEIJER, in MEIJER & ELLIOTT, 1991) and *T. papillosum* (NIYOMDHAM & KUBAT, 1987), both present in my study area.

*T. quadrangulum* was the most common species in the belt where the rafflesia occurred, closely followed by *T. sp. 1*. Elsewhere *T. sp. 1*, *T. papillosum* and *T. lanceolarium* prevailed. Thus, contrary to what I had written (BÄNZIGER, 1988) following BAIN & HUMPHREY (1980), *Tetrastigma* are not rare, at least the species known as hosts of *R. kerrii*. They are often major components of the forest, clearly dominating in some areas.

The stems of many *Tetrastigma* spp. contain significant amounts of water. This rapidly dribbles out if one cuts a section out of the stem and holds it vertically, an activity unfortunately practiced by thirsty forest people because the water is potable, clear and tasteless. The local name for *Tetrastigma* sp. 8 is เถาวัลย์น้ำ (thaowan nam = 'water liana'). All the mentioned species show this feature (though *T. sp. 1* seems to have little water; spp. 6, 10, 11 have not yet been tested). The availability of large amounts of readily flowing water may be related to its parasitism by rafflesias. Its tissue is very spongy and could be 'pumped up' easily without undue loss of nutrients from the host as long as not too many flowers develop on it.

The fruits of the many species of *Tetrastigma* are quite diverse, as must be their seed dispersal ecology. *T. campylocarpum* (Kurz) Planch. has no pulp, but *T. voirnierianum* Gagnep. and *T. quadrangulum* are said to be pulpy and comestible (GAGNEPAIN, 1912, 1930). Fruit size ranges from 0.7 cm (*T. pedunculare* (Wall. ex Laws.) Planch.) to 3.5 cm (*T. hookeri* (Laws.) Planch. (LATIFF, 1984)). The colour is white, yellow, red or black. I found ripe *T. quadrangulum* fruits to surpass 3 cm in diameter. They were shiny bright yellow, strongly perfumed, and the pulp had plenty of sweet juice. Surprisingly, such a 'delicacy' is not eaten by people in the study area because, as they explain, it is not fed upon by animals and hence is not safe (although in N. Thailand it is said to be edible). In an experiment on myself I took a daily increased dose from a tiny drop up to the whole pulp of a fruit (after which my supply ran out — I took the precaution to undergo the trial in Chiang Mai where there are hospitals). Except for a slight throat irritation no detectable ill-effects ensued. I deduce from this that there must be a frugivore which eats this and that in the study area it is likely to be either nocturnal, relatively scarce, or otherwise difficult to detect. Fruits with a strong scent are generally attractive to mammals rather than birds; but being attached to relatively young and slender stem sections hinders the approach of primates and large birds capable of swallowing the whole fruit or at least large chunks containing the 1–3 big seeds. The most likely dispersers are thus bats which may fly directly onto the fruit and take off with the whole of it to eat somewhere else. It is also likely that fruits fallen to the ground are eaten by mouse deer.

In a number of aspects *Tetrastigma* spp. are similar to the liana *Parvatia brunoni-ana* Decaisne (Lardizabalaceae), such as the corky bark with prominent ridges or other structures. Some of the biological features described for the latter (BÄNZIGER, 1989) are likely to apply also to *Tetrastigma*, such as vegetative reproduction by lateral runners. In time these send out rootlets and later become separate plants if severed from the parent

liana, or when the latter dies. Since in some species the runners attain a length of many meters, the liana can actually shift from the original place, and spread. This is of great significance to rafflesias because, if their filaments can infiltrate new runners, they can move and expand the colony (I share this idea with Dr. S. Elliott). However, the opposite is also conceivable, namely, that the host can rid itself of the parasite if the latter cannot infiltrate new runners (from the roots the filaments must be able to penetrate the stem and from there they then have to infiltrate the runners). Large colonies such as No. 1 can be expected to weaken the liana and be the likely cause of death of those roots with all the rafflesia buds. The modest size of rafflesia-parasitized *T. quadrangulum* compared with the maximum size they can attain, may be indicative of a growth slow-down. However, it could also mean that young *Tetrastigma* are more frequently infected than hitherto suspected, either vegetatively through runner infiltration and/or through new infection by the rootlets of rafflesia seedlings (cf. discussion).

### Morphology of the *R. kerrii* Flower (Figs. 1–9, 21–23)

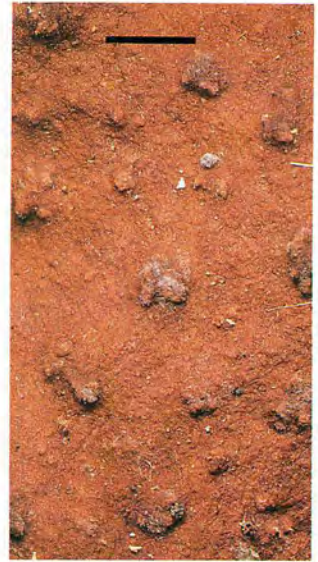
The original description (MEIJER, 1984), based on poorly preserved material, has been considerably improved by MEIJER & ELLIOTT (1991) who examined freshly cut buds. The present analysis adds further details based, for the first time, on fully developed and open, fresh male and female flowers.

Overall colour dull red with brownish tinge. Warts and nodules of perigone lobe in male No. 1 pinkish, in female No. 2 as background or even slightly darker (sexual dimorphism, individual variation, or just discoloration?). Pustules on diaphragm pinkish white. Wall of perigone tube appearing dark, due to the black ramentae and nodules. Annulus exterior, disk and processes shiny and lighter red though the extremities of the latter are darker. Bristles on processes yellowish brown.

Diameter of whole flower 50 cm (female 52 cm) but may attain 70 cm. Perigone lobes 13–18 cm long and 19–22 cm wide, without the white edge mentioned by MEIJER & ELLIOTT for buds. Warts (Fig. 7) on perigone lobe consisting of groups of 2–4 more or less coalescing nodules, with smaller ones randomly dispersed in the spaces between the warts. These are smaller than the spaces between the warts and tend to decrease in size towards the margins. Diaphragm (Fig. 4) curved inwardly with pentagonal outer rim (Fig. 5) of 65 cm circumference (69 cm in female), 4–5 cm wide (4.5–7 cm in female), with great numbers of tiny, irregularly and densely packed pustules about 1 mm across, with centrally ruptured membrane (Fig. 8). At places the pustules draw closer together forming a pinkish-white agglomeration (Fig. 5) surrounded by a reddish halo which can give the impression of a wart (MEIJER mentions 5 concentric rings of warts on the diaphragm). Central opening of diaphragm slightly elliptic, 12 by 17 cm (more roundish in female, 15–16 cm), the underside with bright white, roundish to elliptic blots (Figs. 4, 13) up to more than 10 mm diameter (7 mm in MEIJER and MEIJER & ELLIOTT) though mostly quite smaller. No clear arrangement of the blots in concentric rings seen, nor were any raised on stalks though there were a number of raised, crater-like structures in the area where the blots and the ramentae join. These are maximally 3 mm long (10 mm in MEIJER) with enlarged bifid or trifid tips. Distribution of the ramentae (Fig. 1) variable: within a band of 2–4 cm width, the upper margin of which starts just below the white blotches while the



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7



8



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Figures 6–9. Morphological details of female *R. kerrii* shortly past full bloom. 6, disk with processes; 7, warts of perigone lobe; 8, pustules of diaphragm; 9, process of disk with rows of bristles on crest. Note rapid formation of mold which was nearly completely lacking 24 h earlier (Fig. 6). Length of bar 25 mm in Fig. 6, 5 mm in Figs. 7–9.





10



11



12

Figures 10–11. Buds of *R. kerrii*. 10, medium sized; 11, 19 cm across, some 2 weeks before opening.

Figure 12. *Tetrastigma quadrangulum*, host of *R. kerrii*. Note trifoliate leaves, angulated young stems, and fruits soon ripening.



lower margin ends abruptly (Fig. 13), about where tiny nodules are found down to the annulus exterior. Alternately, the ramentae may be on a broader band where they steadily shorten further down and gradually merge into the tiny nodules mentioned. The annulus exterior is about 2 cm wide; between this and the annulus interior runs a sulcus 2–3 mm wide. The central disk (Fig. 6) is 12 cm across (up to 18 cm in MEIJER & ELLIOTT) with a groove along the rim which is confined by the disk collar of 2 cm height along the crest of which is a row of tiny bristles. On the disk are 29 processes (Figs. 6, 9) (32 in female No. 2, arranged in an outer whorl of 17, a second one of 12 and an inner group of 3; 40 processes in a male bud from Grik) (MEIJER & ELLIOTT have 27–44 processes). They are up to 3 cm long, elliptic at base, tend to be radially compressed, increasingly flattened towards the apex where they are mostly blade-like, 0.5–2 mm thick and up to 2 cm wide, or spike-like; some anastomized and become rather wider. On the crests and tips are rows of bristles nearly 1 mm long (Fig. 9) (not mentioned by the above authors).

The underside of the disk (Figs. 1, 2, 21–23)—described in more detail because of its importance for pollination—shows a number of differences in the two sexes. Unlike the female, in the male the lower rim is more or less rounded, at most with one edge on some sectors in some specimens. The anthers, 5–6 mm in diameter and saddle-shaped, number 28 (36 in a bud from Grik; 26–31 in MEIJER & ELLIOTT). Each is set in a cavity of 6–10 mm width. These are carved out of the underside of the disk and set in a circular row around the column. They open towards the interior and the base of the flower, the anther being in a vertical position with the only pore directed horizontally towards the column. Between the cavities there is a ridge which extends in a radial spire from the anther first up, then in, and finally down before levelling off near the annulus interior as it curves out. The ridges are topped with rows of 1–2 mm long, somewhat stiff hairs (not mentioned in MEIJER & ELLIOTT) which make the ridges impassable and also shield the anther at the distal opening of the cavity. Sparsely distributed hairs are also on the underside of the disk and on the annulus interior where the ridges level off down to the sulcus but not between the ridges. MEIJER & ELLIOTT mentioned additional, 'weak, longitudinal ridges' in the anther cavities; they are lacking or extremely faint in my specimens. In other words, the cavity with the anther is at the end of a grooved, 6–10 mm wide, channel formed by radial, hair-topped ridges starting near the annulus interior and running up in an increasingly steeper curve (Figs. 21–23).

In the female the lower rim of the disk has two well marked edges between which runs an obliquely set, 2–5 mm wide, flat or slightly concave band (Fig. 1). This feature is missing in the male and is very useful for sex distinction (by touch) in the field; it has not been mentioned by the above authors. The anther cavities are replaced by a groove 2–4 mm wide running round along the column. The ridges and hairs are completely reduced and of the channels only faint, narrow, radial depressions remain, if any. The underside of the disk, between the groove and the narrow, oblique band, is covered by a velvety mat of tiny white hairs or papillae; this annular band represents what I believe is the long-sought-after stigmatic surface (cf. discussion). It is set at an angle with the annulus interior and the column, which is without hairs, so that the space between the first and the latter two narrows toward the interior (Figs. 1, 28, 29).

Some of the differences mentioned are partly due to the variability of rafflesias and to the possibility that this most northerly population is subspecifically distinct. The bristles on the processes could be of taxonomic significance. According to KULT (1969) they are absent in *R. arnoldii* but present in other species. They can suffer damage in preserved material, which explains why they may have been overlooked in previous descriptions of *R. kerrii*, and possibly in other species.

### Phenological Notes

The male flower No. 1 (Fig. 4) was discovered in full bloom on 26 January and presumably had been open for 2–4 days. It had slightly damaged perigone lobes, probably nibbled by some insect. Most of the processes were blackish with extensive, irregular patches of yellowish-white mold (Fig. 13); some still had reddish sections. This is not necessarily a sign of deterioration but may contribute to the flower's mimicry of a festering wound. The following day the perigone lobes were starting to curl at the edges and the overall colour seemed a bit darker. Paired marks were detected on the lobes, probably caused by the teeth of a squirrel or rat. After 16 days the lobes had completely shriveled, become dark grey to black, and the inner parts of the tube were rotting.

The female flower No. 2 was found on 12 February as a bud 15 cm in diameter. On 6 March it measured 17 cm across and the pinkish outer side of the lobe was visible between the gaping scales. By 7 April it was slightly past full bloom (Fig. 5). Perigone lobes and diaphragm were more brownish than in male No. 1, the distal 3–10 cm of the lobes darker than the proximal ones and with some greyish white mold, and starting to curl. However, the disk, processes (Fig. 6) and annulus exterior were much brighter red than in No. 1, although the latter was not as old. Small patches of whitish mold were present on some of the processes. The following day most of the processes and disk were greyish black with greyish white mold cover (Fig. 9), showing how fast darkening and mold growth can be. The diaphragm's margin around the opening was greyish, the lobes somewhat further dark. On the fourth day everything inside the tube was blackish, other parts also dark, yet the lobes still had sections greyish brown-red.

The male flower No. 3 was detected on 26 January as a bud 15 cm in diameter. On 12 February it measured 19 cm across and the pink between the scales was visible over about 1/3 of the surface (Fig. 11). On 6 March it was a fully open, but wilting flower (Fig. 19), though still of the original shape, completely grey-black, with plenty of mold, possibly a week or more old. The following day more wilting, curling and mold.

I have not yet been able to study the earliest stages of a *R. kerrii* flower while it is opening up.

### Scent Emanation

Rafflesias are notorious for their carrion-like smell and *R. kerrii* is no exception. Some authors, however, have contested the presence of a putrid smell. HOSSEUS (1907) stated that *S. himalayana* does not smell but in my experience it does, though not strongly so. KUJIT (1969) suggested individual variation and restriction of the smell to a particular stage of the flowering which I found to be the case here.

The stench is generally stated as originating somewhere within the perigone tube. In *R. kerrii*, however, it definitely comes from the perigone lobes, as can be easily verified by close smelling. The diaphragm seems to release less odour, if at all, but this is more difficult to assess since it is so close to the lobes. The smell is not perceptible to the human nose in the cavity of the tube when it is sealed from the outside (cf. experiment below).

I presume the flower starts releasing odour at the latest when the lobes approach their definitive positions, continuing to emanate it as long as the flower is in full bloom. The male flower No. 1 smelled putridly on both days of observation. But, if the female No. 2 represents the norm, the stench ceases soon after the flower is past full bloom, while still reddish. At this stage another, but much weaker, smell is perceptible at the perigone lobes and diaphragm, reminiscent of rancid butter. In the greyish black male No. 3 the lobes smelled more like fermenting bread and mushrooms, evidently due to mold. Buds do not stink internally (when cut open).

The most exciting finding in *R. kerrii* is its 'anticlimax' odour: a pleasant fragrance akin to dried apricots and peaches. It is released from within the perigone tube. It is less intensive and completely overwhelmed by the stronger putrid smell except near the central opening or within the cavity. This was assessed in the following way. Thanks to the size of the flower, I could put the whole of my face into it with the diaphragm closely adhering to the edge of my face—much like a gas mask—thus excluding stench-contaminated outside air from penetrating into the cavity: the fragrance was distinct.

It is intriguing that no such fragrant emanation from blooming flowers has been mentioned for any other *Rafflesia* species. Although it may be unique to *R. kerrii*, I am inclined to believe that it might have been overlooked in some of the species due to the overpowering stench.

It is not yet clear exactly where the fragrance comes from, but a slimy coat covering the underside of the disk, column and adjacent part of the annulus interior of both sexes does have this scent. I am not aware that this wet film has been mentioned for any other rafflesia. The ramentae tested have no such scent.

The fragrance is already perceptible in large buds which have been gnawed open by animals. Even buds severed from the host have this scent for some time; this was also mentioned by MEIJER & ELLIOTT (1991) who assumed the scent would later undergo chemical change into the offensive smell. The fragrance persists throughout and beyond the blooming stage but tends to assume a more fermented by-aroma. In the grey-black stage of male No. 3 it is more fermented and acid.

It is known that in certain flowers emanation of scent is concentrated in particular floral structures. However, *R. kerrii* seems unique in the extent of the scents' contrast and the effects they have on the pollinator.

### Deceptive Flower ?

It is generally assumed that rafflesias are *Täuschblumen*, i.e. deceptive flowers. These attract pollinators by faking the presence of resources required by them. Visitors therefore remain unrewarded for services offered.

I believe that *R. kerrii* may be considered a deceptive flower insofar as the putrid stench deceitfully advertises rotting flesh meals for adult flies and brood sites for their progeny when there are really none. Also, no nectar is apparently offered. However, rafflesias produce large amounts of pollen, part of which is available to visitors entering the more secluded, tenebrous parts below the disk. Moreover, a slimy secretion is available here.

In rafflesias pollen comes in form of a yellow mush (Fig. 18) thicker than milk but more fluid than mayonnaise. The mush is much less viscous than the pollinia of certain orchids, e.g. *Paphiopedilum* spp., which are so sticky that they cannot be sucked up by Diptera (pers. observ.). In the moist microhabitat of the perigone tube the pollen mush retains its consistency but outside the flower where the air is drier, especially during *R. kerrii*'s flowering period, it thickens substantially. This is important for pollination because it can stick as a viscous clot firmly to the dorsum of the thorax of the pollinator (Fig. 15) and be carried around for a long time. I found pollen mush to be tasteless to my tongue and with no detectable scent.

It is unlikely that pollen mush is stolen by calliphorid flies from the anthers as the cavities in which they are set and the channels leading to them are built in such a way that the mouthparts of the flies cannot reach the anthers (Figs. 22, 23) (cf. morphological section). It is also highly unlikely that the pollen clot on the pollinator's thorax is used by females to invite copulation. The vast majority of blowflies visiting *R. kerrii* were females and the clot would be in the right position to be sucked as a 'nuptial' reward by mounting males. 'Wedding gifts' are offered among Empididae (Diptera) and Bittacidae (Mecoptera) (JACOBS & RENNER, 1974). However, in these cases the behaviour is highly ritualized and it is the male which displays the prize. In calliphorids it would at best be a casual occurrence.

However, at least in *R. kerrii* and in *S. himalayana*, the anthers exude 'excessive' amounts of pollen mush, the surplus detaching itself by gravity and dropping onto the annulus interior not far from where the ridges of the anthers' channels level off. Flies can readily imbibe it here. I have noticed drops of fallen pollen mush in mature buds of *S. himalayana* before they opened (Fig. 18) (evidenced by surgery). Such drops were even present in the withering *R. kerrii* flower No. 3, no longer visited by pollinating flies.

So far I have not seen a fly in the act of sucking such drops (they are not visible from the outside) but knowing the flies' pollen-feeding habits (cf. section on their biology) I would be astonished if they did not take it up. That other authors failed to mention the presence of such drops on the annulus does not necessarily mean that other *Rafflesia* spp. do not produce them. The flies indeed might have fed upon them and licked the annulus clean.

Besides pollen mush it is likely that the flies also suck the fragrant, slimy secretion coating the parts below the disk. But, besides moisture, I do not know whether it has any nutritional value to them. It was tasteless to my tongue.



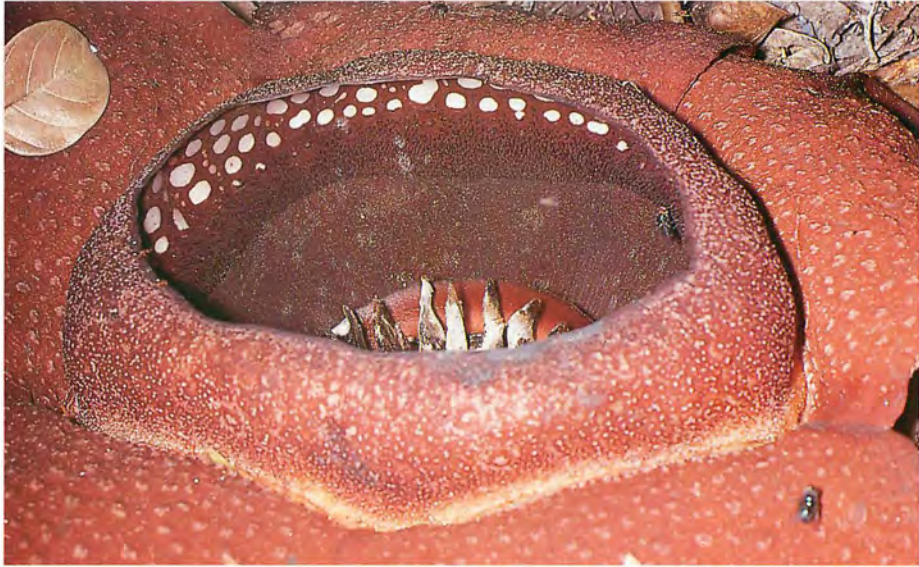


Figure 13. The 'festering sore' appearance of *R. kerrii* (crater shape, lurid and suppuration-like colours), and its carrion stench, attract blowflies: two on the perigone lobe, another at the lower, abrupt end of the band of ramentae. *Drosophilas* are on the rim of the diaphragm and tip of the processes (whitish due to mold), and 2 neriids are on the perigone.



Figure 14. Blowfly *Chrysomya villeneuvei*, female, gazes into the cavity of male *R. kerrii* from the rim of the diaphragm before flying into the cavity.



Figure 15. Female *Chrysomya rufifacies* with a clot of pollen mush on the back of the thorax (arrow), cleaning its hind legs on the edge of the perigone lobe of male *R. kerrii*. Flies are nearly 10 mm long.



Figure 16. *C. villeneuvei*, female, the back and sides dusted with pollen of an unidentified flower, is on the perigone lobe of male *R. kerrii*.





Figure 17. *Hypopygiopsis tumrasvini*, female, on the perigone lobe of female *R. kerrii*.

Figure 18. Cross section through a mature bud of rafflesia (s.l.) *Sapria himalayana* showing yellow drops (arrows) of surplus pollen mush fallen on the annulus interior and wall (bud was inclined to one side hence the 'oblique' trajectory). Length of arrows is 1.3 cm.

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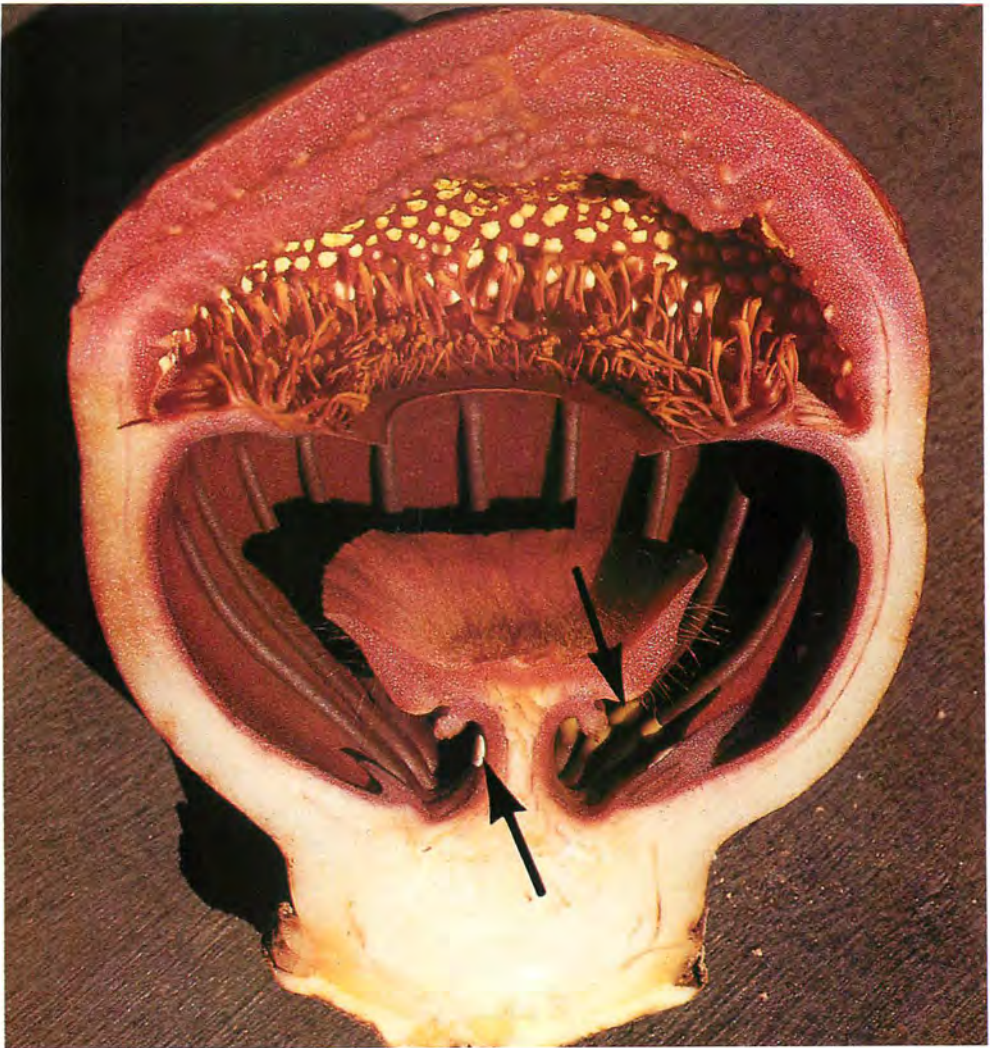






Figure 19. *R. kerrii*, wilting male, possibly a week or more after full bloom. No carrion flies are present, only a single muscid in the cavity and plenty of saprophagous drosophilas.



Figure 20. 13 buds of *R. kerrii* being sold at a fruit stall in Perak, Malaysia. All buds have been cut together with part of the host's roots, a destructive practice.



The frequency and quantity of drops of surplus pollen mush need further study. Nevertheless, since pollen offers carbohydrates, lipids and protein potentially for both energy supply and egg maturation, I believe *R. kerrii* is not really a deceptive flower.

### Arthropod Activity in and around *R. kerrii* Flowers

In order not to interfere with fly activity only a limited number of specimens were caught. Unfortunately, reliable identification of calliphorids requires capture and examination under magnification so it is not possible to give exact individual numbers per visiting species. Arthropod specimens are deposited at DEFACU and the British Museum (Nat. Hist.).

#### Male flower No. 1

Observations on flower in full bloom carried out 1400–1630 h and 1045–1600 h on 26 and 27 January, respectively.

Insects involved in pollination turned out to be calliphorid flies *Chrysomya villeneuvei* Patton, *C. rufifacies* (Macquart), *Lucilia porphyrina* (Walker) and *Hypopygiopsis tumrasvini* Kurahashi. There might have been 5–10 *C. villeneuvei* and *C. rufifacies* to one *L. porphyrina*; only about 4 *H. tumrasvini* were seen. Males were very scarce. Up to 6 flies were seen at the same time on or in the flower, and more were perching on the vegetation nearby. On the first day fly activity was constant, even frenetic at times, some individuals obviously returning several times. On the second day it was much reduced, at times hardly anything moving, probably due to the cloudy weather.

During 2.5 h of observation on the first day 6 *C. villeneuvei*, *C. rufifacies* and *L. porphyrina* females were seen with a clot of pollen mush on the back of the thorax (Fig. 15), 4 of which already had it prior to landing on the flower. During 5 h on the second day the numbers were 8 and 3. Only one *H. tumrasvini* had a small clot on the anterior right corner of the thorax back. The species is rather larger than *Chrysomya* and *Lucilia* spp. and must be hindered in advancing through the channel.

Typically a calliphorid landed onto the perigone lobe, or less often onto the diaphragm, and probed the surface with its labellum for nutrients (Figs. 4, 13). Since these were wanting, the fly drew back its labellum, rested for a while or crawled around and probed a new spot. It might then walk or fly onto the diaphragm, advance towards the rim and gaze into the cavity (Fig. 14), or fly straight into it landing on a process of the disk or more often on the cavity's wall. The labellum probed again. Then the fly might crawl downwards toward the annuli and the darker recesses below the disk out of sight. It circumambulated the disk's column more or less completely as after a minute or so it could be seen to reemerge from another point at the tube's base. In a number of individuals the back of the thorax was smeared with pollen mush. The fly then crawled up the wall, rested, or flew off.

Other flies observed were one *Sarcophaga peregrina* Robineau-Desvoidy and a few individuals each of 2–3 species of Muscidae which settled on *R. kerrii* but did not penetrate below the disk. Flesh-flies (Sarcophagidae) such as *S. peregrina* feed and breed in carrion and other decomposing organic matter, while the Muscidae have more catholic habits. There is no indication that these flies are involved in pollination but *S. peregrina* needs to be investigated further.

*Drosophila* spp., known to be attracted to fermenting organic matter, were very common, and a few individuals of Neriidae (Diptera) were also seen. Some of these entered the tube but none penetrated into the twilight area below the disk. They are unlikely to play any role in pollination because of their small size.

A few individuals of the wasp *Polybioides*, probably *gracilis* v. d. Vecht, a genus new to Thailand, persistently flew around the flower, at times settling on the lobes but not advancing into the tube. They certainly are not involved in pollination. They occasionally landed on my skin and gnawed at it. At least 4 individuals were together with blowflies *C. megacephala* (Fabricius) and *C. rufifacies* (Macquart) on the severed head of a macaque where the wasps were biting off flesh, a behaviour not previously known in these wasps. A specimen was also seen visiting the fragrant inflorescence of *Tetrastigma* sp. 7. Nothing is otherwise known about the biology of these wasps but according to Dr. B. Petersen (*in litt.*) they 'are rather fierce when near the nest with about 2000 specimens'.

A spider of the Salticidae, possibly *Jotus* sp., was lurking on a plant adjacent to the rafflesia; it grabbed and overpowered a *C. villeneuvei*.

Two more calliphorid spp. were present in the study area but, so far, were not caught from *R. kerrii*, viz. *C. pinguis* (Walker) and *H. infumata* Bigot. It can be expected that these, and *C. megacephala* also frequent the flower.

## Female flower No. 2

Observations of flower somewhat past full bloom made during 0920–1700 h, 1115–1700 h and 1030–1300 h on 7, 8, and 10 April, respectively.

On the first day calliphorids arrived as late as 1020 h and the last ones left about 1515 h. An estimated 5 *C. villeneuvei*, 20 *L. porphyrina* and 6 *H. tumrasvini* (Fig. 17) visited the flower. Some individuals, especially *H. tumrasvini*, made repeated attempts to enter the tube. None had pollen on the back.

The behaviour of the calliphorids on this female rafflesia, which discontinued to emanate carrion stench, was in stark contrast with that observed on the male No. 1 with its putrid smell. Of the 31 individuals only 12 (2, 7, 3 specimens of the species mentioned above in this sequence) flew into the perigone tube; of these only 6 (2, 3, 1) did actually settle (on disk, processes, wall) while the other 6 flew into and out again without landing. Most importantly, none proceeded down into the obscure recesses below the disk. As discussed in the following section, these blowflies appear to need preconditioning by carrion-like stench to advance into dark cavities.

No calliphorid was detected visiting the flower the following days.

Other insects frequenting the flower were as mentioned for the male, including a *S. peregrina* on the first day. New visitors were 4 *Therates kraazi* Horn (Cicindelidae). Tiger beetles are known to be aggressive predators of other insects and *T. kraazi* probably were lurking for prey attracted by the flower's scents.

### Male flower No. 3

Observations on this wilting, grey-black flower still retaining much of its original shape were carried out during 1000–1300 h on 6 March, 0930–1000 and again 1530–1600 h on 7 March.

No calliphorid fly was seen on the flower although I did see them visiting fresh human faeces in the area. On the first days a *S. peregrina* and one neerid fly settled briefly on the lobe; a muscid fly (Fig. 19) did so on the inner wall where there were plenty of mites. At least two species of drosophila, viz. *D. sulfurigaster* Duda and *D. albomicans* Duda, were flying around the rafflesia. On the second day no insects but great numbers of drosophila were around, especially on the disk.

A dry and shrivelled bud of colony No. 1 which must have died while half open, had plenty of ants inside. One bud of colony No. 4, which died shortly before blooming due to a hole gnawed by some rodent, had a blattid inside. Other shriveled flowers had termites in their bases.

### Biological Notes on the Fly Pollinators

For clarification of the mechanism of pollination in *R. kerrii* it is necessary to understand certain aspects of the flies' physiology and behaviour. Only data pertinent to fly pollination are mentioned. Calliphoridae (blowflies) such as *Calliphora* (bluebottles), *Lucilia* (greenbottles) and *Chrysomya* are fairly well researched because of their importance as health hazards. Adults are attracted to meat, carrion, faeces and other decaying animal matter for egg laying and/or feeding. The larvae of *Chrysomya bezziana* Villeneuve and *Lucilia sericata* Meigen are parasites in wounds, abscesses and body cavities of man and animal (SMITH, 1973)

A number of workers on pollination ecology have overlooked the fact that flower visiting and/or sucking of sugary plant sap is essential for adult carrion flies (cf. Fig. 16). They frequent especially Umbelliferae (STEINER, 1948), Rosaceae, Euphorbiaceae and Compositae (KUGLER, 1951), Salicaceae and Araliaceae (SCHREMMER, 1963). Except for the Compositae, where they presumably feed mainly on pollen (KUGLER, 1951), on the other families mainly nectar is taken. Calliphoridae play a role as pollinators in fruit orchards such as mango (*Mangifera indica* L.) in Thailand (SUARNAYATHIPAT, 1984). Another food calliphorids eagerly feed upon is sap of fruit, especially if fermenting (STEINER, 1948).

Sugars are the main energy suppliers for both males and females, while protein is needed for egg maturation. Females of *L. sericata*, *L. cuprina* Wiedemann and *C. rufifacies* require at least one meal of protein to lay eggs (MACKERRAS, 1933). But meat alone is a poor source of nourishment for both males and females. While *L. sericata* die within 2–3 days if given water but no sugar (WIGGLESWORTH, 1972), they lose weight and also die relatively soon if given meat and water alone. They increase in weight and live 1–2 months if given sugar and water but no meat; addition of meat will increase weight and age only slightly in males though in females the weight rises significantly due to egg maturation (not available for energy supply) (EVANS, 1935). It is clear that a diet of sugars and meat is best for both sexes but especially for the females.

Pollen offers carbohydrates, proteins, lipids and other nutrients which could cover all the adult flies' nutritional needs; however, I have found no reference analyzing the actual value of pollen for calliphorids. There is little doubt that despite the chemically resistant walls of the pollen, its nutrient content can be digested by the flies' enzymes penetrating through the germination pores of the pollen, as is the case with bees (STANLEY & LINSKENS, 1974).

The average age of *Lucilia* in captivity was 7 weeks but they can live over 3 months (SALT, 1932; MACKERRAS, 1933). Calliphorids are energetic flyers and recapture of marked individuals has proved that they can fly distances of 22 km within a few days (BISHOPP & LAAKE, 1921). Because of these two features, I think these flies should be considered as potential long distance pollinators, comparable, on a lesser scale, to the euglossine bees (DRESSLER, 1968; JANZEN, 1971), an important factor for rare plants such as rafflesias.

According to KUGLER (1970) in *Lucilia* and most other insects, attraction to flowers from a distance is optically guided while at close range olfaction is more important. Exceptions are attraction to flowers emanating carrion, excrement and other smells of decaying animal matter which work as long distance lures. In experiments (KUGLER, 1956) showed that carrion flies are drawn to brownish red colours in the presence of carrion or faeces smells but not when it is absent. AUTRUM & STUMPF (1953) proved experimentally that, unlike bees and many other insects, *Calliphora erythrocephala* Meigen is able to see red as a colour. In the absence of fetid smells, yellow and white are the most attractive colours for calliphorids (KUGLER, 1951). They are likely to act at medium and close range in rafflesia. At medium distance they may help make the otherwise essentially reddish *R. kerrii* more conspicuous. The white blotches on the underside of the diaphragm are visible at low level flight, the moldy yellowish white patches (if present) on the disk's processes at higher level. At close range, from the edge of the diaphragm, the recurring white blotches on the dark underside of it could act like a checker model. The black-and-white checker design has been shown to be more attractive than a pale grey or dark one (STEINER, 1948).

Wrinkled surfaces, warts, filaments, processes also appear to exert attraction (KUGLER, 1956). VOGEL (1961, 1963) pointed out that in most cases processes like those on the disk, besides being optically attractive, also release scents from special glands, the osmophores of Arcangeli. The rows of bristles on the crests of the processes may be indicative of such osmophores. The nodules and ramentae might also draw attention optically.

As mentioned by VOGEL (1961) Diptera generally are known to react with positive phototaxis when in dangerous or unfamiliar surroundings—they move toward the light. However, an observation I have made on carcasses of monkeys in the study area is of importance. *Chrysomya megacephala* and *C. rufifacies* readily enter dark recesses, cavities and holes when on carrion. Its smell seems to condition them not to be scared of darkness. The observations on rafflesia No. 2 (previous section) indicate that without previous conditioning by stench such calliphorids do not advance into darkness.



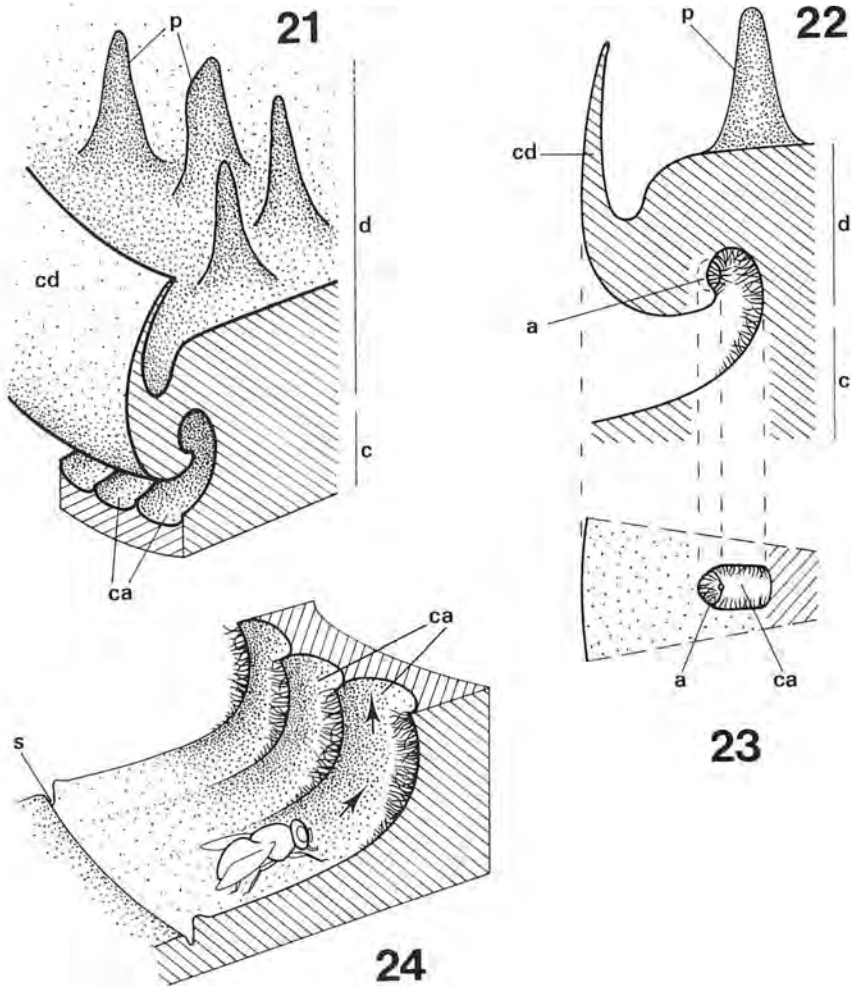
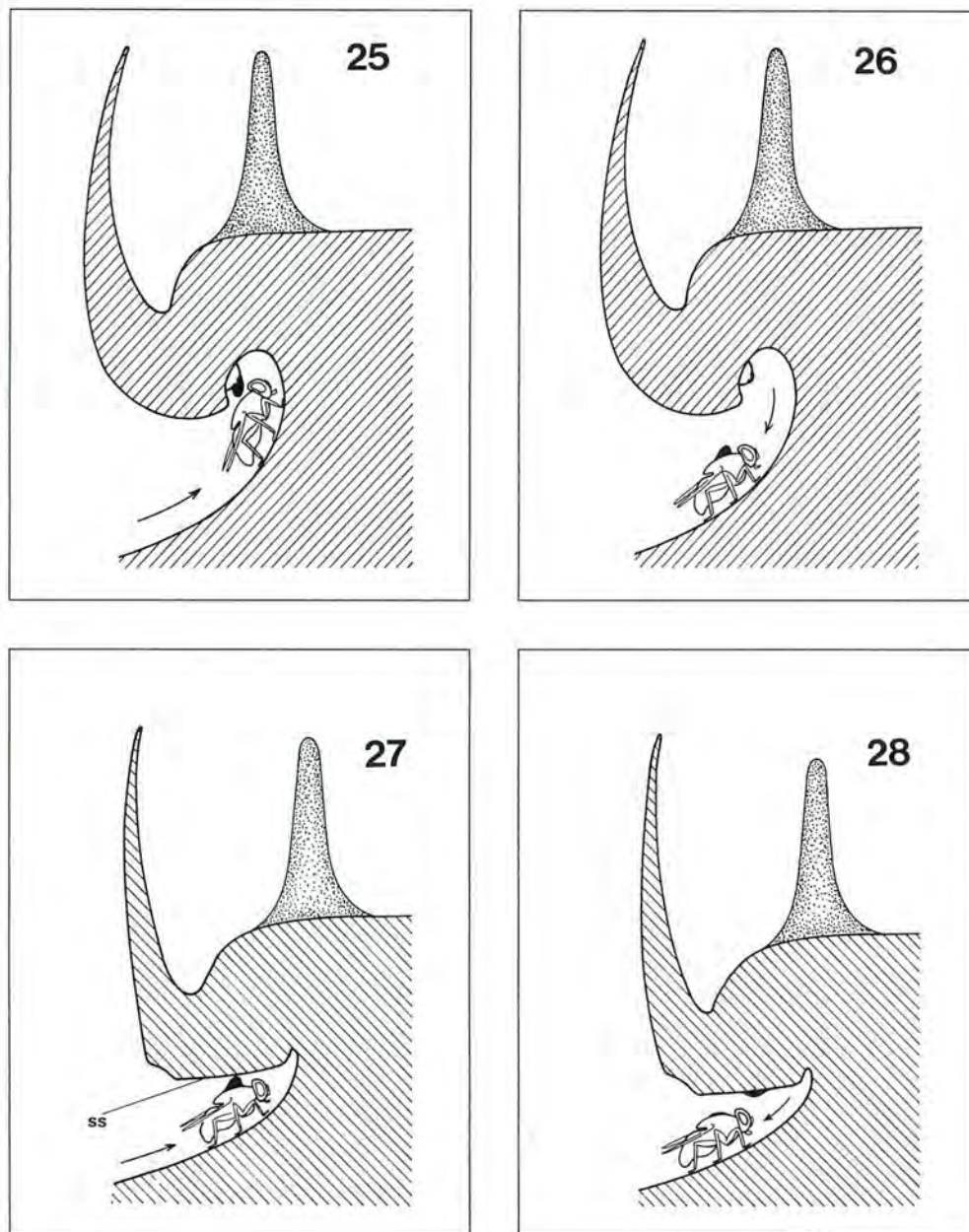


Figure 21. Oblique view of cross section of disk and column (part) of male *R. kerrii* depicting the general situation of the pollination sequence shown in Figs. 22 – 28 (Figs. 27 – 28 are of female which lacks the channels). Schematic; proportions in all drawings not to scale.

Figure 22. Cross section of disk and column showing details of hairs lining the channel leading to the anther.

Figure 23. View of a disk sector from below, showing the position of anther and hairs which protect its access from three sides.

Figure 24. Calliphorid fly entering a channel leading up to an anther. Oblique view; disk omitted. a = anther; c = column; ca = channel leading to anther; cd = collar of disk; d = disk; p = process; s = sulcus.



Figures 25 – 28. Pollination of *R. kerrii*. Above: male (hairs omitted); below: female. 25: Calliphorid nearing the end of the channel just before the back of the thorax touches a drop of pollen mush hanging from the anther. 26: After a short advance the fly retreats taking along a clot of pollen. 27: Calliphorid with clot of pollen climbs the wedge below the disk bringing the clot near the stigmatic surface (ss). Further advancing will cause the clot to be brushed off the stigmatic surface. 28: The fly retreats leaving behind most of the pollen.

### The Pollination Mechanism (Figs. 21–28)

From a distance of probably many dozens of meters a pollinator calliphorid encounters a whiff of the putrid smell from a *R. kerrii*. Following the gradient it flies toward the source of the smell and perceives the lurid reddish colour. Olfaction is now assisted by vision including the white of the blotches on black background and/or white patches (if any present) on the processes. The fly locates the flower and settles on a perigone lobe. As neither tarsi nor labellum sense any rotting food, it crawls around to find a more promising spot. Upon climbing or flying onto the diaphragm, when near its margin it can see the checker design and the processes, both attracting the fly towards the cavity of the tube, especially if the processes are moldy ('festering sore' appearance). The insect flies into the tube, landing first on a process or directly on the wall. Here the putrid smell is weak or absent while the stronger fruity fragrance announces plant food; the fly crawls down below the disk. (Movements below the disk were not seen; the following sequence is a deduction based on morphological and behavioural evidence, combined with analogous mechanisms in other flowers.) The fly crawls around the column, presumably probing the slimy film and sucking pollen mush (if any left by earlier visitors) dropped down near where the channel to the anther starts. Searching for more it climbs up the channel (Figs. 24, 25) until near the end the back of the thorax comes into contact with the pollen mush hanging from the anther. Further advance is obstructed by the cavity's wall, and turning is prevented by the narrowness of the channel. While retreating, it will take along a clot of pollen mush on the thorax (Fig. 26). It may search for more food or come out from below the disk, walk around, or fly off.

In the female flower the whole process is presumably the same up to the moment the fly crawls under the disk. Slime is possibly sucked. Given the lack of channels on the column, the fly can proceed in any direction but will tend to climb the narrowing wedge (Fig. 27) between the annulus/column and the stigmatic surface. Sooner or later the back of the thorax is brought into contact with it, smearing or rubbing the pollen clot (if any is present) off onto the velvety mat of the stigmatic surface (Fig. 28).

### DISCUSSION

It is perhaps typical for rafflesias that the elucidation of the pollination mechanism had to wait for more than 150 years although there was little doubt about it ever since DELPINO's (1873) fundamental work on pollination. DELPINO recognized eight types of insect pollination systems (and 45 groups of flower scents!) and characterized the *sapromiofile* (sapromyophilous) flowers thus: display lurid colours (reddish), have cadaveric stench and are pollinated by carrion flies—all salient attributes of rafflesias. Of course many researchers have proposed flies as pollinators. The reason for the interregnum are the difficulties connected with the study of blooming flowers and the other peculiarities of the parasite mentioned in the introduction.

The location of the stigmatic surface had likewise remained uncertain (KULT, 1969). But there are compelling morphological and functional reasons for assuming that the annular band on the underside of the disk is the stigmatic surface. The whitish mat of hairs or papillae with which it is covered is typical of the stigmatic area of some other flowers (KUGLER, 1970). Considering the pollination syndrome from a functional aspect,

the annular band seems to be the only area where the pollen clot can possibly be smeared off the back of the calliphorid fly.

It has been mentioned that only smells of decaying organic matter act as long distance flower attractants in pollinating insects. Other scents work at close range and flowers generally have to rely on visual lures for long distance attraction. If this is so, then in the dense vegetation of tropical forests stenchy flowers have a selective advantage over fragrant ones, however optically conspicuous they may be, since visibility is reduced there. This may help explain why smell-producing flowers like *Rafflesia*, *Aristolochia*, *Amorphophallus*, *Sauromatum*, *Masdevallia* and others are exclusively or mainly found in the tropics. The *Stapelia* of the S. African semi-deserts would seem to contradict this but because of their specific habitats a different explanation may apply in their case. Stenchy plants in the temperate zone seem to grow mainly where there is thick vegetation, as is the case with the stinkhorn (*Phallus impudicus* L. ex Pers.) (SCHREMMER, 1963).

I follow FAEGRI & PIJL (1979) in viewing sapromyophily as a more recent development than other pollination systems. Stench, as an evolutionary 'new decoy' is a more effective lure than fruity fragrance, yet the latter has not become obsolete in *R. kerrii*. Its possible function may be in continuing to advertise carbohydrate food to prevent calliphorid flies from being misled by the stench to lay eggs in an unsuitable brood site. It is not in the flower's interest to kill off prospective pollinators or to endanger the development of its own fruits and seeds by inviting oviposition by flies the larvae of which could be destructive. In fact, while the larvae of the mentioned Calliphoridae normally develop in decaying animal flesh they probably can survive in other decomposing organic matter as many of their relatives are known to (SMITH, 1973). Larval *C. bez-ziana* infest mammalian sores but will readily invade and devour healthy, live tissue (SMITH, 1973) and *L. sericata* is so voracious in this that it eventually causes the death of sheep (DÖNGES, 1980). *L. porphyrina* has apparently been reported to cause fatal myiasis in toads (WYATT, *in litt.*) which were healthy initially. Moreover, little-known flies such as *H. tumrasvini* or other, not yet observed, rafflesia-pollinating calliphorids may have larvae with more catholic tastes than the ones so far seen on *R. kerrii*, and accept decaying plant tissue. Difference in the pollinating fauna, e.g. presence of more stenophagous larvae, may explain why rafflesias in Malesia are without fruity fragrance. However, unless females are under 'egg-laying' stress due, for instance, to long-delayed opportunity to lay, oviposition is often induced only by a combination of stimuli perceived by the antennae, labellum, legs and/or ovipositor. It may therefore be questionable whether blowflies would be misled into laying in rafflesias, whatever the scents.

Nevertheless, there are a number of documented cases of 'misled' oviposition especially in stapelias (FAEGRI & PIJL, 1979; KUGLER, 1970), the orchid *Paphiopedilum rothschildianum* (Reichb. f.) Stein (ATWOOD, 1985), with subsequent larval death reported in *Aristolochia grandiflora* Swartz and other *Aristolochia* spp. (CAMMERLOHER, 1923). The opposite is also known where the brood of the pollinating fly developed normally in the male *Alocasia pubera* (PIJL, 1953). Even in *R. kerrii* maggots have been mentioned (KERR, in MEIJER & ELLIOTT, 1991) in old flowers. Moreover, I have found tiny larvae in rotting males. I suspect they were drosophilids or other saprophagous flies living upon decomposing plant matter. A rich saprophagous fauna and flora is only to be expected in such large rotting flowers.

Perhaps the presence of the fragrance in *R. kerrii* but lack in other rafflesias can be explained from an evolutionary perspective. *R. kerrii* could be a link between the more primitive pollination system based on scents advertising nectar and/or pollen, and the derived sapromyophily of more advanced rafflesias of Malesia, where speciation has been more rapid. *R. kerrii* would have developed stench production in the perigone lobes but not in the cavity where it retained the fragrance; for pollination an olfactory lure is necessary to attract flies into the innermost, dark part of the flower. Malesian rafflesias might have advanced further, replacing the fragrance with stench. Fragrance as an 'oviposition deterrent' may be an advantage, but not vital, at least in Malesia. Detailed future research may prove that minor amounts of fragrance continue to be emanated from the cavity of some Malesian rafflesias.

My view that *R. kerrii* is not really a deceptive flower would receive further impetus if the interpretation that the fruity fragrance keeps flies from laying eggs should prove correct. In the light of the above, the function of such a strange structure as the diaphragm may be to keep the stench off from the tube and prevent the fragrance from too fast diluting out of it. It also works somewhat as a roof to reduce rainwater falling into the interior, assisted to some extent by the disk—centered exactly below the diaphragm's opening—the high collar keeping the water on the disk. Waterlogging is a lesser problem for *R. kerrii* and *S. himalayana* which elegantly solved it by flowering when rains are sporadic. It is not yet understood how Malesian rafflesias cope with this problem (cf. JUSTESEN, 1922 and WINKLER, 1927). Finally, the white blotches on the dark background of the underside of the diaphragm probably work as an attractant. In my view the blotches should not be interpreted as 'light windows' (as in KUIJT, 1969). LINDNER's (1928) light windows of *Aristolochia lindneri* Berger, CAMMERLOHER's (1923) of *A. grandiflora*, VOGEL's (1961) of various *Ceropegia* spp., and TROLL's (1951) of yet other species, are diaphanous structures with a specific function, viz. to illuminate an otherwise dark recess of the flower. This is necessary to draw phototactically positive flies to that particular section. The blotches in rafflesias are wrongly located for that function which would be, in any event, useless for the calliphorids since they readily enter dark areas, at least when conditioned by stench. Also, while indeed diaphanous to some extent, the blotches are more effective in reflecting the light.

KUIJT (1969) commented that animals ranging from ants to elephants have been suggested to act as dispersal agents of rafflesia seeds. In my study area the mouse deer may be involved besides squirrels. The latter have been reported to eat the fruit (MEIJER, 1958). MEIJER also suggested that they carry the seeds on their feet and effect inoculation when their claws penetrate the bark while the squirrel climbs a new *Tetrastigma* liana. Inoculation may be more likely to occur during rummaging by wild boar (MEIJER, 1958) but they were not present at my study sites. I think that the soil fauna, mainly arthropods and nematodes, may be more effective. Myriads of them populate the upper humus-rich soil strata. Many of them gnaw, scratch and suck from rootlets, leaving wounds, often microscopic, through which the tiny root filaments of the seedling could penetrate *Tetrastigma* roots. It is not impossible that the earliest stage of the rafflesia seedling may enter into some kind of beneficial relationship with soil fungi until its rootlets can infect a *Tetrastigma*. The relatively modest size of infected *T. quadrangulum* may be an indication that infection by seedlings' rootlets is more common than suspected (cf. also other explanation

in section on hosts).

It has been assumed (e.g. MEIJER, 1958) that for successful pollination of rafflesias, male and female flowers must be present at the same time, and obviously not too far from each other, a serious drawback for such short-lived, rare flowers. In the light of the new results above, it is clear that pollination may occur with flowers blooming many days or weeks apart, although the effectiveness must diminish with time. The pollinating calliphorids are long-living, strong fliers, and the pollen clot firmly sticks to the back since the pollen mush solidifies to some extent in the outside air. They could act as long distance pollinators. It would be conceivable, albeit extremely unlikely, that pollen from a flower in Prachuab Khirikhan in January could be delivered onto a female in Surat Thani, several hundred km to the south, three months later in April. Thus, even isolated, single rafflesias can play a role in helping conserve a species and they should not be written off. Yet the present study indicates that for long-term survival rafflesias are dependent on an unusually diverse array of factors: a forest rich in the required *Tetrastigma* spp.; suitable frugivorous bats, appropriate terrestrial and arboreal mammals for dispersal of *Tetrastigma* seeds; sufficient medium to large sized mammals (e.g. primates, ungulates, etc.) to provide, once dead, brood sites for larvae of calliphorid pollinators (carbohydrate food for the adults should be no problem for generalists like calliphorids); possibly squirrels and small terrestrial mammals as dispersing agents of rafflesia seeds; and a healthy layer of soil and humus rich in soil fauna which I suspect is the main agent allowing new host infection. Any conservation program for rafflesia has to consider these conditions *in toto* to be effective in the long term.

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### Appendix 1. *R. kerrii* in Ranong Province, S. Thailand

On 13 April, 1991, 2 buds 7 cm across and a rotten male flower which did not open fully were found growing on a large individual (15 cm across stem) of *Tetrastigma* sp. 12 (same sp. as Bänziger coll. No. 941 of that neighbourhood). This is another new host for *R. kerrii*. The place is at 150 m elevation, in an evergreen forest. Following calliphorids were present: *Catapicephala sinica* Fan, *Hemipyrellia ligurriens* (Wiedemann), *Hyppogyropsis infumata*, *H. tumrasvini*, *Lucilia papuensis* Macquart and *L. porphyrina*. Local gum (*Dipterocarpus* sp.) tappers were aware of the rafflesias in the area. They collect them for sale to a nearby temple for up to 100 Baht depending on the size. The resident monk prepares concoctions for various purposes.

### Appendix 2. *R. kerrii* in Upper Perak State, W. Malaysia

In Baling a total of some 25 buds were on sale at two street stalls selling fruit, for 10 M\$ each (Fig. 20). I was told they come from the deep forest in the area.

In Grik a dozen buds were on sale in a traditional medicine pharmacy. According to the seller, Orang Asli from the forest bring them in by the *hundreds* during the 'dry season' months of October to December. Concoctions are given to pregnant women but they are also invigorating to men. Also on sale were two medicine preparations, a syrup ('Faizol tonic') and pills ('pill buasir'), containing among other ingredients, rafflesia extracts.

Both Baling and Grik are about 20 km from the nearest frontier with Thailand. Although it is most likely that the plants came from within Malaysia, it cannot be excluded that the forest-roaming Orang Asli have taken them from Thailand. Nevertheless the above records are the first from Malaysia.

### Appendix 3. *R. kerrii* as a tourist attraction

MEIJER & ELLIOTT (1991) proposed *R. kerrii* as a new Thai tourist attraction in order to save it from extinction. They support the idea with a number of convincing arguments. 'Ecotourism' with rafflesia has met with some success in Sumatra (though there are cases where colonies have been badly trampled by too many visitors). It seems feasible that with appropriate financial investment and expertise a sensible 'ecotourist' development project could be implemented with rafflesias at sites not too far off roads, where the environment is already degraded.

Nevertheless, I wonder about the wisdom of exposing such rare and sensitive flowers to the whimsical tourist business. We are only just starting to understand rafflesia's ecology, still know nothing about its propagation, and cannot yet cultivate it. Nature education deserves all-out support but why put endangered species at risk? There is so much else, less vulnerable, to show and educate about.

What I fear most is that 'ecotourist' promotion of rafflesias in the marginal habitats will lead to an increased threat to the populations deep in the forest, the most pristine and only viable ones in the long term. I doubt these can – or actually should – be saved by 'ecotourism'. It would be an ordeal for the average tourist to be brought to a population

like the one I studied, and hence it is likely that it is the rafflesia which will be brought to the tourist.

Thailand is different from Sumatra. Tourism is far more advanced and is spilling into every corner of the kingdom. The communication network is capillary and for the most part good to excellent. Thai people are far more enterprising (a very positive trait on most counts) but this is coupled with an unusually liberal *laissez-faire* attitude towards what is permissible and lax law enforcement. On top of this comes the devastating success with which the Tourist Authority of Thailand has been able to promote mass tourism. Rafflesias already have a market value due to their purported medicinal properties and they do not need another from tourism. Thus the best populations could be in serious danger of being wiped out by local collectors of forest produce, many of whom understandably need additional income. As mentioned by MEIJER & ELLIOTT (1991) there is already a small souvenir business with rafflesias. Collectors rarely are aware of the dependency of the parasite on the liana and will cut its stem to make passage easier and sever roots (Fig. 20) when taking the buds or flowers.

(Shortly after I had written the above lines, marauders wiped out the only population I knew of the rare slipper orchid *Paphiopedilum parishii* (Reichb. f.) Stein — object of a long term study which I had been carrying out for a year already. The site was in a wildlife sanctuary and much less accessible than the *R. kerrii* population.)

In the case of Thailand I would like to propose a moratorium until scientists have mastered a technique to cultivate rafflesias. Then perhaps they can be grown in the landscape gardens of luxury hotels and resorts—under appropriate glass cover lest the stench and carrion flies scare their customers away.