NAT. HIST. BULL. SIAM SOC. 43: 337–365 , 1995

ECOLOGICAL, MORPHOLOGICAL AND TAXONOMIC STUDIES ON THAILAND'S FIFTH SPECIES OF RAFFLESIACEAE: *RHIZANTHES ZIPPELII* (BLUME) SPACH

*Hans Bänziger**

ABSTRACT

All 22 clusters of *Rhizanthes zippelii* studied in Thailand (where it is confirmed for the first time) and in W Malaysia parasitized exclusively *Tetrastigma pedunculare* (Wall. ex Laws.) Planch. (Vitaceae) although other *Tetrastigma* spp. were also present, some reported as hosts elsewhere. The morphology and ecology of the host liana are detailed. Mostly its only connection with the ground was by aerial roots and *R. zippelii* generally grew on these near ground level. Morphological evidence indicates that *R. lowi* (Beccari) Harms, described from buds, is best synonymized with *R. zippelii*, a rather variable species. From extrapolation of growth measurements, buds would need some 200 days to reach a circumference of 3.7–4.1 cm (when they break through the host bark) from a swelling of 0.5 cm diameter, and another 200 to maturity when 14.7–20.5 cm in circumference. Flowers start to open around midnight and are fully open around noon the following day (although insects first visit during early morning) and remain fresh for 2–3 days. The mush-like pollen is generally depleted in the first day but pollinating flies (Calliphoridae, Diptera) continue to visit for many days. The pollen mush clots and hardens once smeared by flies onto their back. Experiments show that hardened pollen mush retains substantial germinability for many days and that clotting is readily reversed when swept over the fluid-soaked stigma. Nectar is exuded near the tip of the perigones. A 'stuffy room' odour comes from the perigone/column and a weaker excrement/cheese-like smell from the caudate appendages. *R. zippelii* is a sapromyophilous flower which acts mainly by brood-site deception.

INTRODUCTION

An encounter in a steamy rain forest with a flowering *Rhizanthes zippelii* makes an intruder wonder. The look of the flower is more akin to a tentacled animal—a starfish or medusa—than to a member of the plant kingdom. But at the same time the reddish globe with crater, embedded in a tangle of rufous hairs, reminds one of the blood-shot orifice of a furry mammal. This perplexing aspect is part of an intricate set of lures: visual, tactile, olfactory and gustatory, as treated in a second study on the plant's pollination syndrome (BÄNZIGER, 1996).

The present state of knowledge of *Rhizanthes* Dumortier has been aptly reviewed by MEIJER & VELDKAMP (1988), with data on its nomenclatural history, morphology and anatomy (e.g. SOLMS-LAUBACH, 1876, 1898; HEINRICHER, 1905; CAMMERLOHER, 1920), seeds (SOLMS-LAUBACH, 1874, 1898), pollen morphology (TAKHTAJAN ET AL., 1985), cytology (PIJL, 1933), geographic distribution and, as far as the sometimes deteriorated and

*Department of Entomology, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand, 50200

incomplete museum material allowed, detailed taxonomic description.

Previously known, among else, mainly under *Brugmansia* Blume, at present two species are recognized, viz. *R. zippelii* (Blume) Spach and *R. lowi* (Beccari) Harms, distributed in Sumatra, W Malaysia, Borneo and, for *R. zippelii,* also Java (MEIJER & VELDKAMP, 1988). The present study proves the presence of *R. zippelii* in Thailand for the first time, a finding which is not entirely unexpected as the species is included in a list of Thai plant names (SMITINAND, 1980). However, Dr. T. Smitinand informed me that he had never seen the plant, despite his life-long field experience; that the record originated from his predecessor; and that there is no herbarium material from Thailand (if any had ever been collected). Furthermore, the record remains dubious also because one of the local names listed was the same as that for *Rafflesia kerrii* Meijer, *bua phud* (บัวผุด) with which it might have been confused, while another is *bua khrang* (บัวครั่ง). The present study increases to four the number of genera of Rafflesiaceae present in Thailand, the other three being *Sapria* Griffith (with two included species), *Mitrastemma* Makino and *Rafflesia* R. Brown (with one Thai species each) (HOSSEUS, 1907; HANSEN, 1972a, b; MEIJER, 1984; BÄNZIGER, 1991).

Less is known about the biology of *Rhizanthes* than the still poorly understood *Rafflesia* and *Sapria* while *Mitrastemma* has been comprehensively researched by WATANABE (1936, 1937). The bud phenology of *Rafflesia* and *Sapria* is known to some extent (MEIJER, 1984; ELLIOTT, 1990, 1992), as is the pollination biology of *Rafflesia* (BEAMAN ET AL., 1988; BÄNZIGER, 1991) though it is poorly known in *Mitrastemma* and unknown in *Sapria.* Seed dispersal and host infection are still a matter of speculation for all of them. For *Rhizanthes,* among the least known of the nine genera of Rafflesiaceae, even morphological aspects and taxonomy are far from elucidated. This is perhaps due to its variability, complicated by the peculiar presence of bisexual as well as male and female flowers, as already noted by SOLMS-LAUBACH (1876) and HEINRICHER (1905). Other reasons are its secretive mode of life and a disconcerting, to some people even repulsive aspect, with hairs which look like they could sting and appendages which, during the opening phase of the flower, resemble the trap spikes of a carnivorous plant. This did not endear it to local people or the occasional collector.

The most detailed biological notes so far have been on the longevity of 2 or 3 flowers and their odour, made on four occasions by F. Bartel (HEINRICHER, 1905). Several authors have commented on the smell produced by the flower. Visiting insects were identified as carrion flies, fruit flies, gnats, ants, etc. DELPINO (1868) attempted a first interpretation of the pollination mechanism.

STUDY SITES AND HABITATS

The study areas consisted of three sites in evergreen rain forest. The most northerly was in Sukhirin District, Narathiwat Province, South Thailand. The other two were between Gopeng and Chenderiang, South Perak, Peninsular Malaysia, the general area mentioned by MOLESWORTH ALLEN (1968).

Site (a) in S Thailand was along a 5–15 m wide stream in a 20–50 m broad gully meandering southwards to westwards, at 260–340 m msl (mean sea level). 13 clusters of

R. zippelii—four only with dead buds or desiccated flowers but possibly with live thalli inside the host—were distributed over a distance of about 1 km. The clusters were less than 3 metres from the stream though two were about 10 m from it. The forest (Fig. 1) was variably shady with estimated total daily sunflecks reaching the clusters from a minimum of 1/2 to a maximum of 2 h.

Site (b) (shown to me by Mr. M. Wong) was a north-flowing, 15 m broad, shallow stream bed strewn with stones, gravel and various plants at 330 m msl. The water flowed between and below them; after heavy showers they would be briefly be inundated. Much of the area was covered by a species of Araceae. Despite careful checking of the surroundings only two clusters of *R. zippelii* were found, 30 m apart, both in the stream bed, where the vegetation was most open. Thus, while the soil was perpetually wet, the habitat received more light than the average understorey vegetation, with sunflecks reaching the flowers for about 2–3 h daily.

Site (c) was in a separate valley about 2 km from site (b) and consisted of 7 clusters (2 shown to me by an Orang Asli, 5 found by myself) strewn over about 1/2 km, in a narrow gully along a stream, 350–450 m msl, exposed SE to SW. The habitat was essentially the same as that of (b) but more shaded. Sunflecks nevertheless reached the clusters for up to 1/2 h daily. One cluster was on rocks in the stream bed, the others on adjacent gravelly banks a few metres from the stream.

The area of study in S Thailand is under the influence of the east coast weather regime —heaviest rain in November and December, followed by a relatively dry period in March–May with low rainfall. During 30 March to 17 April 1995 only 4 late afternoon showers were experienced. Mid-day temperatures were 26–30°C and relative humidity (RH) was 65–90 % (quite high considering that it was the 'dry' season, obviously the result of humid, nearly constant, though slow wind drifts down along the stream). The minimum night temperature was 21°C at 100% RH. Humidity is of paramount importance for the clotting of the pollen mush (cf. chapter on pollen).

At the sites in Perak, exposed to the west coast weather regime, there is a period with low rainfall in January and February and again in June and July when there are generally many days without rain. However, the periods during my studies in January and February 1994 and 1995 were unusually wet with most days cloudy at least in the afternoon and with rainfall during more than half the 26 days of research (night rains not considered). Relative humidity was generally 85–100% but when sunflecks reached the clusters it was reduced to about 75%, and occasionally was as low as 65% when wind came from sunny ridges instead of down the humid gully. Between 0930 and 1930 h temperatures were 22–25°C. The rainy weather experienced was unfortunate as a single shower destroys the reproductive ability of male *R. zippelii* flowers by washing away the pollen; furthermore, pollinator activity is reduced.

The quest for *R. zippelii* in Thailand began on 18 March and the last observation was on 18 April, 1995. The Malaysian sites were visited on 9 days during 24 January to 3 February, 1994, and 16 days during 15 to 31 January, 1995. Flower watching for pollinators was carried out during 29 days for a total of 140 h, about half of which were at the Thai sites.

Unfortunately, none of the three sites is in a protected area. As during other studies on endangered species in Thailand, I worked alone and refrained from asking locals about

the possible presence of the plant in their area to avoid giving the plant a marketable value. My discovery of the plant was the result of systematic search for the appropriate host liana in suitable habitats. The study sites in Malaysia were relatively safe thanks to Mr. M. Wong and the Orang Asli who were aware of the advantages of protecting them.

Collected material is at present at the author's department but eventually it will be deposited at the Forest Herbarium, Bangkok.

HOST–PARASITE RELATIONSHIP

Hosts infected by *Rhizanthes zippelii*

SOLMS–LAUBACH (1876) mentioned *Tetrastigma papillosum* (Bl.)Planchon (as *Cissus papillosa* (Vitaceae)) as the host of *R. zippelii* in Java. PIJL (1933) reported it on the root of a *Villebrunea* sp. (Urticaceae) in Sumatra. MEIJER & VELDKAMP (1988) added *T. lanceolarium* (Roxb.)Planchon, which is also the species most often infected by *Rafflesia* though, according to LATIFF & MAT-SALLEH (1991) and Latiff (pers. comm.), this name is a junior synonym of *T. leucostaphylum* (Dennst.)Alston. However, more recently Latiff (pers. comm.) concluded that the appropriate name for this most frequent host species of rafflesias is *T. tuberculatum* Bl. I have used *Tetrastigma* sp. 12 for this taxon (e.g. BÄNZIGER, 1991). MOLESWORTH ALLEN (1968) reported *R. lowi* — corrected to *R. zippelii* by MEIJER & VELDKAMP (1988) — on *Kadsura lanceolata* King (Schisandraceae) a finding which is questioned by MEIJER & VELDKAMP (1988). In fact, MOLESWORTH ALLEN'S tracing of the host in the tangle of lianas was uncertain. Furthermore, as shown in a very different study (BÄNZIGER, 1989, Fig. 15), some Schisandraceae like *Kadsura heteroclita* (Roxb.)Craib, have stems with corky ridges, a feature typical of some *Tetrastigma* spp., which might have caused confusion.

R. lowi was mentioned by MEIJER & VELDKAMP (1988) as occurring on *T. dubium* (Laws.) Planchon, *T. glabratum* (Bl.)Planchon and *T. papillosum,* though not on *T. lanceolarium.*

In my study areas, both in Thailand and Malaysia, the hosts of all 22 clusters of *R. zippelii* were *T. pedunculare* (Wall. ex Laws.)Planchon (e.g. coll. No. 1202, 1307, 1308, 1328, 1330) (Figs. 15–17). This species, known from Malaysia, Sumatra and Borneo, is herewith newly recorded for Thailand, where I found it in Yala, Pattani and Narathiwat provinces (e.g. coll. No. 1321, 1327). Furthermore, it is also a new host record.

At the sites in Malaysia, an estimated 1 in 2–4 *T. pedunculare* lianas were infected with *R. zippelii;* in Thailand this was much lower.

Morphological and Ecological Notes on the Host Plant

Below is a description of *T. pedunculare* in the live state. Special attention is given to stem characteristics, a feature often omitted in previous descriptions. Stems are particularly useful for species recognition by the ecologist in the field.

The stem of the liana, round in cross section and up to 4 cm in diameter, is relatively soft and lacks corky ridges or plates so often seen in other *Tetrastigma.* The bark is very

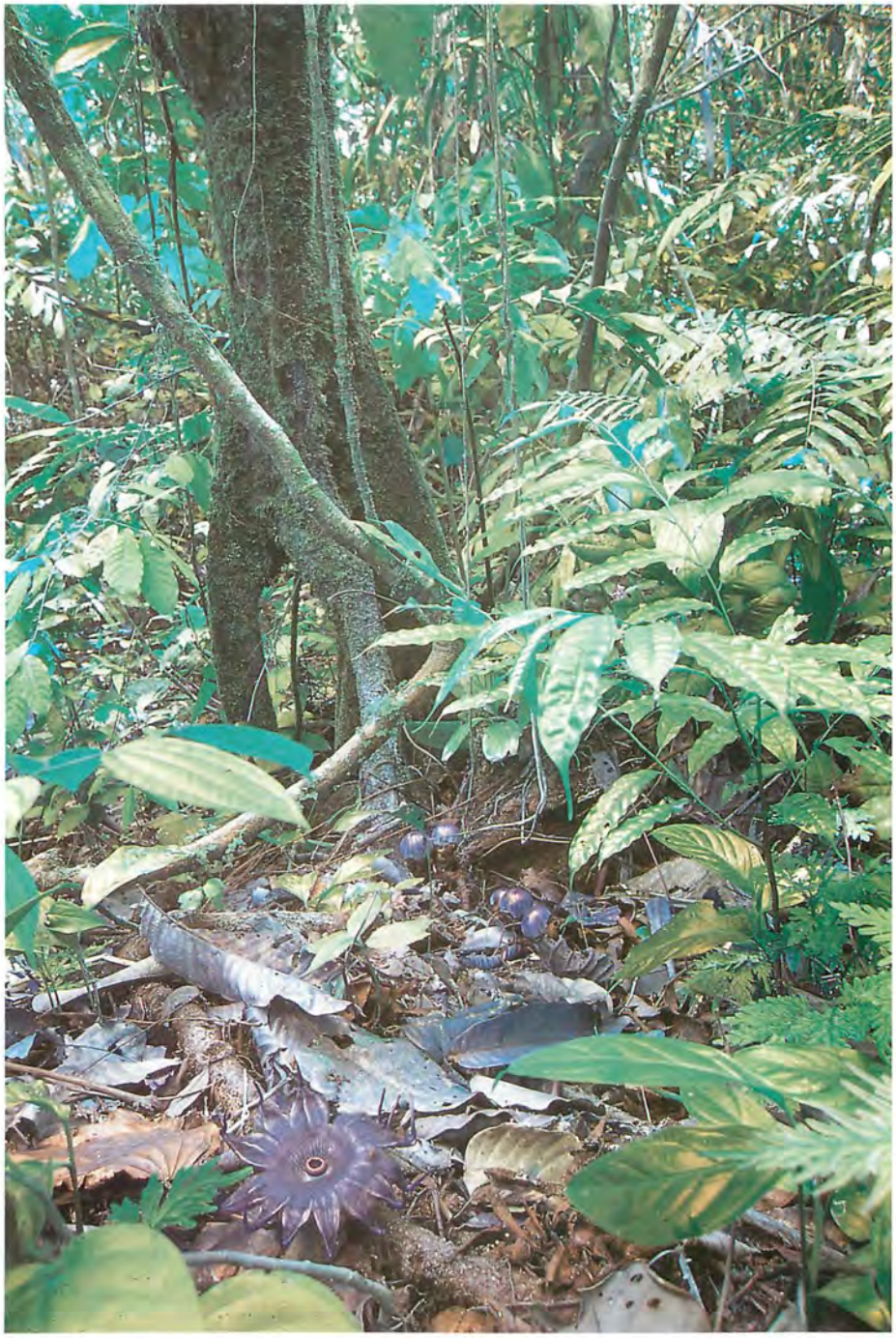

Figure. 1. *R. zippelii* in its typical habitat in S Thailand. A flower in full bloom is at left bottom, five large buds are in the background.

Figure. 2. A freshly opened male flower of *R. zippelii*. S Perak, Malaysia.

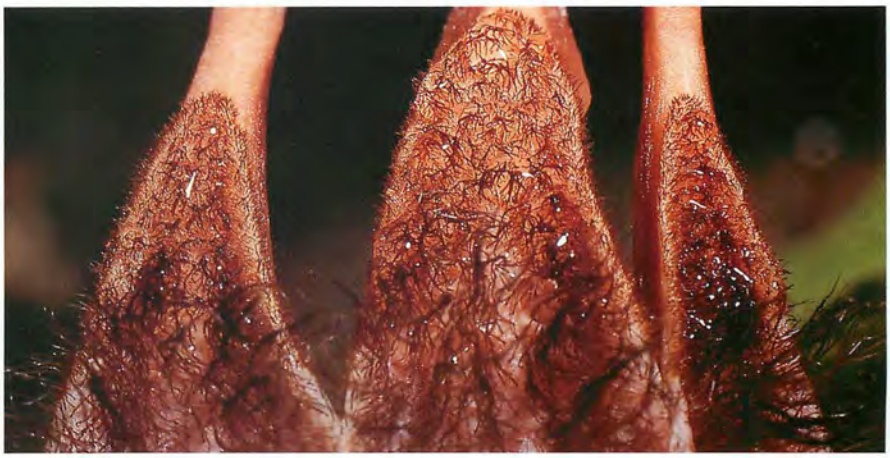

Figure. 3. Glittering droplets of nectar soak the ramenta and part of the tuft hairs near the tip of three perigones.

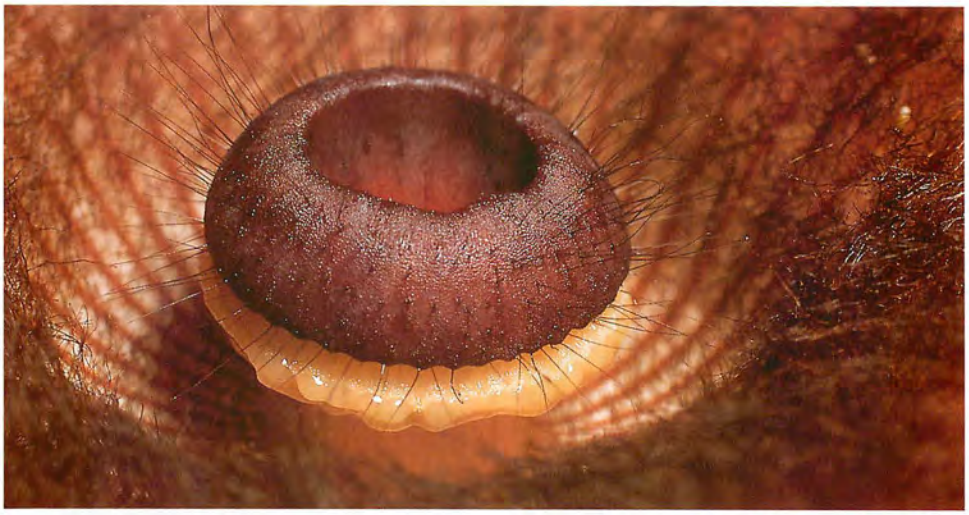

Figure. 4. Ampulla with ring of anthers of male *R. zippelii*. Note the irregular band of yellow pollen mush consisting of merged droplets.

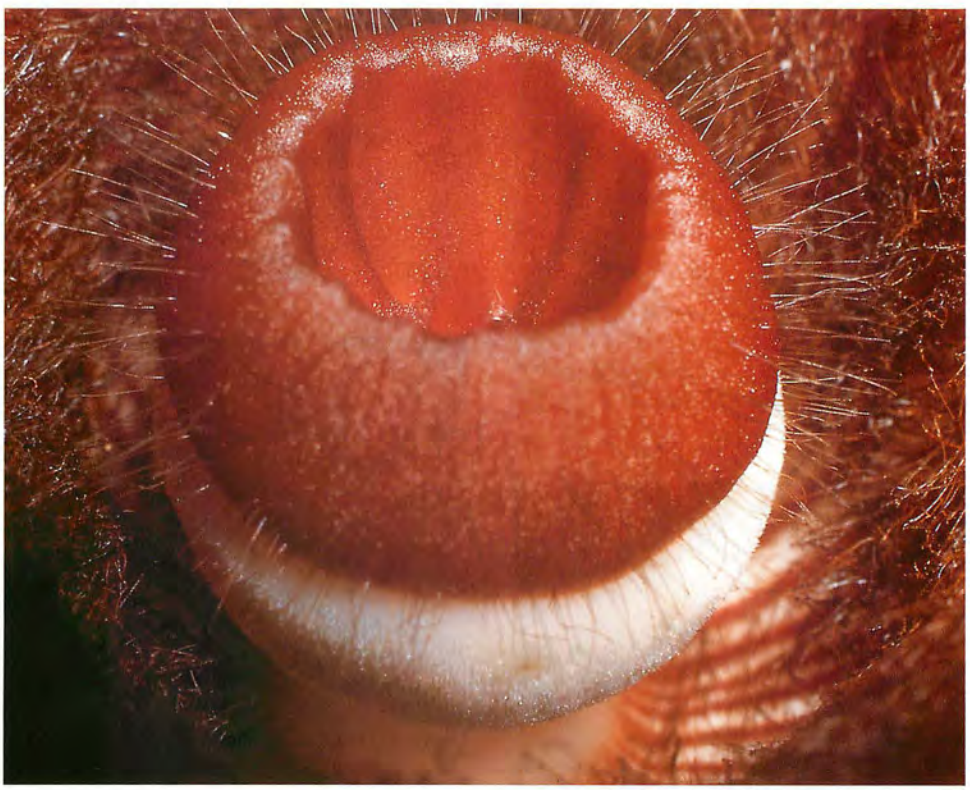

Figure. 5. Ampulla and stigmatic fascia in female *R. zippelii*. Note the white papillae.

Figure. 6–11. Opening phases of *R. zippelii*. 6. Bud 12 h before opening; note the diverging bracts. 7–11. Buds/flowers about 2, 4, 6, 8 and 9 h after the opening started at midnight.

thin, of greyish to brownish colour except where covered by lichens (infrequent in other species of the genus) and is more or less lenticellate. Tissue immediately below the bark is red. I have found this feature only in few *Tetrastigma,* e.g. in *T. laoticum* Gagnep., *Tetrastigma* sp. 22 (coll. No. 1199). The stem is more elastic than in other species of the genus. The sound emitted by the liana when bent, the 'crackling' so typical for *Tetrastigma* (and some other Vitaceae), is somewhat less distinct.

A single large liana may produce dozens of aerial roots hanging down in straight threads to the ground, from as high as 20 m in the canopy, to just a few cm above the ground. The aerial roots (Fig. 17), often only a few mm in diameter, can grow as thick as the stem itself, for which they are then often mistaken. If they are torn, secondary aerial roots develop at or near the wound. Typically, aerial roots do not emit any 'crackling' sound when bent, are rather more reddish below the bark and generally more strongly lenticellate than the stem. The lenticels can be quite conspicuous, occasionally like small tubercles which might lead to confusion with the stem of *T. papillosum* by the non-specialist. The aerial root system resembles that found in *Tinospora crispa* (Lour.) Merr., *Tinospora baenzigeri* Forman (Menispermaceae) (BÄNZIGER, 1982) but in *T. pedunculare* it is more impressive: large old specimens have lost all contact with the ground via the primary root system, the stem growing high up and extending over several tree crowns; the only connection with the ground is by the aerial roots. None of the many specimens found in S Thailand had direct contact with the ground through primary roots and in Malaya only very few did.

Another important feature is the production of lateral runners, present to varying extent also in a number of other *Tetrastigma* spp., e.g. *quadrangulum* Craib & Gagnep., *obovatum* Gagnep., *laoticum, tuberculatum, curtisii* (Ridley) Suesseng., *hookeri* (Laws.)Planchon, as well as other lianas such as *Parvatia brunoniana* Decne. (Lardizabalaceae) (BÄNZIGER, 1989, 1991, and unpubl.). In a single growing season *T. pedunculare's* lateral runners can cover a distance of 25 m. At various intervals along the runner, rootlets develop and if the runner is severed when old enough, it develops into an independent plant. If it is assumed that after 5 years or so a new plant is large enough to produce its own runners and the sequence is repeated for 50 years, then the plant may have 'travelled' some 250 m as a separate but genetically identical plant. It is probable that the parasite 'hitch-hikes' along with it and that nearby clusters of *R. zippelii* belong to genetically identical individuals, derived from a single original thallus.

The leaves are 3-foliolate (Fig. 15), crenate, with very broad leaflets (width more than half the length), with asymmetrical lateral leaflets and short petiolules (less than 1.5 cm long).

The flowers (Fig. 16) are greenish-yellow, very fragrant, the cyme generally dichotomous, often born on the old stem, but mostly high up. The fruits (Fig. 15) are slightly compressed dorso-ventrally, dark red when mature and, at 6–8 mm in diameter, among the smallest in *Tetrastigma.* They tasted sour. The seeds, yellowish to greyish to dark brown, are 3–5 mm in diametre, more or less cordate, with variably crenate margins and typically with a T-shaped endosperm. Further taxonomic features are as mentioned in LATIFF (1984).

In South Thailand many individuals bore profuse fruit during late March to April. In Perak only one plant had fruits but it also had flowers at the same time in mid-January.

It would therefore appear that in both Thailand and Malaya the liana fruits in the dry season and that the simultaneous presence of fruits and flowers in the Perak specimen may be due to the presence of two 'dry' seasons there, the second being in June-July, presumably when the January flowers will bear their fruit. I found the liana at 200–700 m elevation but could not check higher up. It was more common at 200–400 m. It lives in a very specific habitat, namely along perennial streams of small to average size. Individuals often crossed the stream in the canopy, the aerial roots hanging down on both sides of, and into, the stream.

Population Structure of *Rhizanthes zippelii* on its Host

In S Thailand *R. zippelii* grew exclusively on aerial roots of the host, all at ground level except a few which were not more than 30 cm above ground. In Malaysia all buds of the two largest clusters similarly developed only on the very large aerial roots (the stem of both hosts, without primary root connection with the ground, was no less than 15–20 m above the ground at the lowest point). Most of the 15 buds of another cluster developed on the stem of the host and some on the aerial roots. In the remaining 6 clusters all buds developed on roots but it could not be determined whether on primary or aerial ones. Most buds were just below, at or just above ground level, but some were nearly 1 m above ground and 5–6 m from the point where the aerial root entered the ground (after coming down in a wide curve and following the ground for several meters). Two small clusters were on roots in close contact with the rock facies of large bolders. The largest cluster, near a tall tree, was so thickly covered by leaf litter that only the flowers which had pushed aside the leaves while opening, and the tip of some large buds, emerged.

The size of the host root on which *R. zippelii* grew ranged from 1 to 4 cm in diameter. Buds could be so close each other as to mutually impair growth and flowering.

Two of the 22 clusters were solitary, the others occurred in groups of 2–12 clusters, the distance between clusters being 10–30 m. The smallest recognizably live cluster had only one live bud (besides withered flowers), the largest cluster (site (c)) had, over an area of 1 m^2, at least 30 small to large buds and 10 tiny ones still embedded in host tissue; nearby satellite clusters of the same host had about half as many additional buds. Total number of buds seen in Thailand was more than 100 and in Malaysia well over 170.

Four of the 13 Thai clusters had only old, long since withered flowers and it is not clear whether the parasite thallus was still alive inside the host. The remaining 9 clusters had live buds and four had also flowers (only fresh enough ones still visited by flies considered here). All 9 Malaysian clusters had live buds and 6 had flowers. Skeletonized, black remains of flowers which must have withered months before were present in most clusters.

Considering all flowers (fresh and old: 29) and buds (15) analyzed, the sex ratio was 1 female to 3 males. In 5 clusters both sexes were present, in one there were 2 males, in 4 only one individual could be sexed and in the remaining clusters the sex of the parasite could not be established. If reinfection of a host is indeed as rare as is generally assumed—but this is by no means sure—the sex distribution would indicate that *R. zippelii* is likely to be monoecious. A similar situation apparently applies to *S. himalayana* (ELLIOTT, 1992, and own observ.) but possibly not to *Rafflesia* where clusters tend to be of one sex only.

MORPHOLOGICAL AND PHYSIOLOGICAL NOTES ON *RHIZANTHES ZIPPELII*

Functional Morphology of the Flower

The flower morphology is treated mainly from the functional aspect because of its importance for the second part of my study on the pollination. Nevertheless, morphometric data (Tables 1–3) are included because they might prove useful for the clarification of the taxonomic status of *R. zippelii* and *R. lowi* (cf. discussion). No significant difference was noted between the Thai and Malaysian plants, especially when considering the overall variability of the species.

Diameter of the whole flower (Fig. 2) is 11–17 cm, not including the brownish-red, filiform, caudal appendages 2.5–5.1 cm long attached to the tip of the perigone lobes at a right angle (geniculation). The 16 perigones are generally detached from adjacent ones about in the middle of their length though some do not separate at all while others separate nearer the base. Various swellings (calli) may be present on the distal half of the perigone. Near the tip of the perigones there is a narrowly triangular, nectariferous pad 0.8–1.1 cm long and 0.6–1 cm wide on which the ramenta are set. On the basal half the perigones form a campanulate tube which internally merges with the circumambulator, a circular channel (cf. Figs. 4, 5) running round the base of the column. (The circumambulator is so called because pollinators walk in it around the column.) 31–52 brownish-red radial lines stretch from the base of the pale circumambulator to the upper tube where they fade into the more brownish coloration of the distal part of the perigones. At the center of the flower is the pale yellow column consisting of a stalk about 0.5 cm long and a globular head 1.2–2.1 cm wide and 0.7-1.8 cm high. The upper half of the globe is formed by the brownish-red ampulla (Figs. 4, 5) with a crater depth of 0.8–1.6 cm. The lower half of the globe consists of the reproductive organs (described below). The flower is connected to the host via the 'neck', a section containing the ovary (rudimentary in males), set between the insertion of the perigone bases and the cupula (the disk-like attachment of flower and host). The neck is covered by 3 whorls of 5 black bracts (scales).

Females are distinct from males in the following characters (cf. Tables 1–3): Generally shorter caudate appendages (2–3.3 cm vs. 2.5–5.1 cm), shallower crater depth (0.7–1 cm vs. 1.1–1.6 cm), larger (higher and wider) globular head (1.4–1.8 and 1.6–2.1 cm vs. 0.7–1.1 and 1.2–1.7 cm), and more massive neck (3.2–4.4 cm vs. 2.0–2.9 cm) which is also differently shaped. Namely, in the female the walls are parallel or, more often, slightly converging upwardly so that the neck is narrowest just below the perigone insertion. In the male neck the walls converge downwardly (cf. Fig. 6), thus it is narrowest further down near where the last whorl of scales is attached.

There are four types of hairs. (1) Finely pointed, straight, sparse hairs up to about 1 cm long. Brown in colour, they are on the outer wall of the ampulla (Fig. 4) and span the gap between this and the furry hairs of the tube wall. It would appear that their main function is, thanks to a certain stiffness, to keep 'unauthorized' insects - mainly flies such as Muscidae, Platystomatidae, etc.—from intruding into the gap where they might adversely affect pollination, e.g. getting stuck, scaring off pollinators, or stealing pollen. Blow flies are robust enough to deflect these hairs and penetrate deeper.

(2) 'Furry' hairs, cinnamon brown in colour, up to 1.1 cm long, with hooked, bifid,

Table 1. Morphometric data of *R. zippelii* from site (a), S Thailand. Sizes in cm.

Specimen code	Female flower 5.W	Female flower 9.1	Male flower 3.V	Male flower 5.Z	Male flower 5.1	Male flower 5.2	Male flower 5.8	Male bud 11.2
Diameter of flower (geniculation to geniculation)	17	11.5	16	14.5	14	13.5	14	-----
Circumference of bud	-----	-----	-----	-----	-----	-----	-----	13.6
Length of caudal appendages (geniculation to tip)	2–3.3	2.3–2.9	?–5.3	3–4	3–4	3–4	2–3	2–3.2
Width of perigone lobes	1.1–2.0	1.0–1.5	1.9	1.1–2	1.3–1.6	1.3–1.9	1–1.6	-----
Column height (base to crest of ampulla)	2.2	1.9	damaged	1.6	1.45	1.4	1.3	1.25
Width of stalk of column	1.2	0.8	0.8	0.8	0.8	0.8	0.8	0.6
Ampulla height (reddish part)	0.8	0.7	damaged	0.6	0.5	0.5	0.5	0.6
External diameter of ampulla (at maximum width)	1.8[1]	1.6	damaged	1.7	1.6	1.5x1.7	1.4x1.5	1.35
Diameter of ampulla crest (crater aperture)	0.95x1	1	damaged	0.95x1	0.9x1	0.8x1.1	0.75x0.9	0.7
Crater depth (crest to bottom, measured internally)	1	0.9	damaged	1.5	1.5	1.5	1.2	1.2
Width of stigmatic fascia or annular row of anthers	1	0.75	damaged	0.4	0.3	0.3	0.4	0.35
Number of anthers	-----	-----	damaged	48	51	50	45	-----
Width of neck	4.4	3.5	2.6	2.9	2.5	2.8	2.4	1.9

Remarks: [1] stigma wider than ampulla: 2.1 cm. Specimens 5.W, 5.Z, 5.1, 5.2 and 5.8 are all from the same cluster while 3.V, 9.1 and 11.2 are all from different clusters.

Table 2. Morphometric data of *R. zippelii* from site (b), Malaysia. Sizes in cm.

Specimen code	Female flower 0.3	Male flower 0.1	Male flower 0.2	Male flower 0.4	Male flower 0.5	Male flower 0.6	Male flower 0.7	Male flower 1.5	Female bud 1.2	Female bud 0.8	Female bud 0.9
Diameter of flower (geniculation to geniculation)	13	4	12.5	15.5	13	14.5	12.5	13.5	-----	-----	-----
Circumference of bud	-----	-----	-----	-----	-----	-----	-----	-----	17.4	13.6	14.5
Length of caudal appendages (geniculation to tip)	2.8	3.5–4.5	damaged	3.5–4.5	damaged	3–4	2.5–3.5	3.5–4.5	2.7–3.1	1.9–2.3	1.5–2
Width of perigone lobes	1.1–1.8	1.1–1.8	0.7–1.3	1.2–1.9	1–1.9	1.2–1.8	1–1.7	1–1.8	-----	-----	-----
Column height (base to crest of ampulla)	1.8–2.0	1.55	1.5	1.6	damaged	1.45	1.3	1.6	1.9	1.75	1.6
Width of stalk of column	0.9	0.7	0.7	0.8	0.7	0.8	0.7	0.7	0.9	0.95	0.95
Ampulla height (reddish part)	0.8	0.6	damaged	0.6	damaged	0.55	0.5	0.5	0.7	0.6	0.6
External diameter of ampulla (at maximum width)	1.8x2	1.5	1.2	1.5	damaged	1.5	1.3x1.4	1.4	1.75	1.75	1.8
Diameter of ampulla crest (crater aperture)	0.9x1.1	0.9x1	damaged	0.8	damaged	0.9	0.7x0.85	0.85	0.95	0.85	0.9
Crater depth (crest to bottom, measured internally)	1.0	1.3	1.4	1.5	damaged	1.3	1.2	1.2	0.8	0.7	0.6
Width of stigmatic fascia or annular row of anthers	0.7	0.35	damaged	0.35	damaged	0.3	0.3	0.35	0.65	0.63	0.6
Number of anthers	-----	36	damaged	41	damaged	39	46	41	-----	-----	-----
Width of neck	3.5	2.3	2.0	-----	2.0	2.0	2.0	2.4	3.1–3.4	3.4	3.4

Remarks: all specimen are from the same cluster.

Table 3. Morphometric data of *R. zippelii* from site (c), Malaysia. Sizes in cm.

Specimen code	Male flower 2.2.0	Male flower 2.4	Male flower 2.5.2	Male flower 2.5.1	Male flower 2.5.28	Male flower 2.7.1	Female bud 2.5.3	Female bud 2.5.30	Male bud 2.6	Male bud 2.1.3	Male bud 2.1.1
Diameter of flower (geniculation to geniculation)	14	14.5	14	13	13	13	-----	-----	-----	-----	-----
Circumference of bud	-----	-----	-----	-----	-----	-----	15.7	10.7	16	15.7	15.7
Length of caudal appendages (geniculation to tip)	3–4	3.8–5.1	damaged	3–3.5	2.5–3.5	4	2.6	1.7	3–3.8	2.4–3.4	3.0–3.4
Width of perigone lobes	1.1–1.9	1.3–1.9	1.5	1.2–1.5	1.1–1.7	1.1–1.6	-----	-----	-----	-----	-----
Column height (base to crest of ampulla)	1.5	1.5	1.6	1.35	1.45	damaged	-----	-----	-----	-----	-----
Width of stalk of column	0.95	0.7	0.7	0.8	0.7	damaged	0.8	0.65	0.7	0.8	0.7
Ampulla height (reddish part)	0.7	0.55	0.6	0.43	0.5	0.6	0.6	0.4	0.45	0.45	0.45
External diameter of ampulla (at maximum width)	1.7	1.4	1.4	1.6	1.4	1.5	1.9	1.65	1.45	1.5	1.5
Diameter of ampulla crest (crater aperture)	1x1.1	0.9	0.8x0.9	0.8x0.9	0.9x1	insect damaged	1.0	0.6	0.8	0.8	0.8
Crater depth (crest to bottom, measured internally)	1.6	1.2	1.2	1.1	0.95	insect damaged	0.7	0.45	1.2	1.2	0.8
Width of stigmatic fascia or annular row of anthers	0.4	0.4	0.3	0.3	0.35	0.35	0.6	0.55	0.3	0.35	0.3
Number of anthers	47	40	damaged	48	46	damaged	-----	-----	-----	-----	-----
Width of neck	2.3	2.2	2.3	2.4	2.1	2.2	3.2	2.5	2.0	2.0	1.9

Remarks: specimens 2.5.1, 2.5.2, 2.5.3, 2.5.28 and 2.5.30 are from the same cluster, as are 2.1.1 and 2.1.3, while 2.2.0, 2.4, 2.6 and 2.7.1 are all from different clusters.

trifid or multi-branched endings. They are wildly intertwined (Figs. 4, 5) in a tangle covering the perigone from the base of the circumambulator to the tuft hairs in a somewhat loose, wholy mat 0.2–0.5 cm thick. The branched endings obvioulsy mutually anchor their position. The tangle leaves a circular gap of 0.4–0.8 cm between it and the column. I propose that this tangle mimics, at least tactically, the fur of a mammal. At the same time it also works as a device for efficient pollen acquisition and delivery: it elastically presses intruders of the circumambulator against the anthers or stigma when they negotiate the circular gap.

(3) Tuft hairs (BECCARI'S (1869) *ciuffi*), somewhat darker, shorter (0.8 cm), though thicker than the furry hairs and generally lacking branched endings so that they do not form an intertwined tangle but stand out more or less straight upward as well as laterally, somewhat like in a bundle of wheat (Fig. 2). They are found between the furry hairs and the ramenta and cover the width of the perigone for about 0.5 cm. Most authors have not distinguished these hairs from type (2) probably because they worked with preserved flowers; in this the hairs' peculiar posture is lost. I propose that they function as a barrier—not very efficient perhaps—against visitors (except the strongly-built calliphorids) in order to reduce attempts to proceed to the centre of the flower where they might cause damage or disrupt the pollination process. Also, since some of them get soaked in nectar, they may increase volatilization and hence improve attraction; many insect visitors fly only to the nectar.

(4) The ramenta (antler hairs), again essentially similar to type (2) but very much shorter (0.1 cm), are somewhat thicker-walled, darker and likewise provided with single or multiple branchings. Being shorter, they are not so intertwined and form a dark brown velvety carpet. They are distributed distally to the tuft hairs, on the nectariferous pad (Fig. 3). Their function may be to soak up the nectar and possibly to improve its volatilization.

Anthers and Stigma

All 29 flowers and 15 buds of *R. zippelii* examined proved to be either male or female. In regions like Java most *R. zippelii* are bisexual while a few are unisexual, either purely so (SOLMS-LAUBACH, 1876) or with more or less strongly reduced organs of the opposite sex (HEINRICHER, 1905). In bisexual plants the anthers are located directly below the stigma from which they are separated by an annular depression. In my populations the yellowish white anthers are set on the lower half of the globular apex of the column, just below the ampulla (Fig. 4). The 31–52 anthers are arranged in a circular row 0.3–0.4 cm wide. They are curved radially as well as tangentially, resulting in a rib-like appearance of the row. They have a depression somewhat below the upper end where a drop of pollen mush collects and merges more or less completely with that of adjacent anthers. This conglomeration gives rise to a continuous but irregularly thick ring (Fig. 4) of pollen mush which protrudes from the anthers, ready to be sweapt off by pollinators entering into, proceeding along, or leaving, the circumambulator. The free gap between the anthers and the furry hairs is about 0.4–0.8 cm but it can be elastically widened by intruders as the tangle of furry hairs, 0.2–0.5 cm thick, is not stiff.

The correct location of the stigma was pointed out by SOLMS-LAUBACH (1876) but its position was later misinterpreted by most authors until HEINRICHER (1905) and MEIJER &

VELDKAMP (1988) recognized the right position again. The accuracy of this location is also proved by SOLMS-LAUBACH'S (1876) discovery there of germinated pollen and by my experiments with pollen germination (see below).

The stigmatic surface is a 0.7–1 cm wide fascia arranged around the lower half of the globular apex of the column, just below the ampulla (Fig. 5)—essentially in a position corresponding to that of the anthers. The stigma is bright white, at close look somewhat glittering due to the innumerable papillae which give it the appearance of a velvety mat, rather similar to the stigmatic area in *Rafflesia* and *Sapria,* though in the latter ones it is more horizontally set and less radially curved. The free gap intruders have to negotiate is comparable to that in the males.

An important finding is that, while in most flowers the stigma is covered by a sticky film, in *R. zippelii* and even more so in *S. himalayana, Ra. kerrii* (*Rafflesia* is shortened to *Ra.* to distinguish it from *Rhizanthes, R.*) and *Ra. cantleyi* Solms-Laubach, there is an abundant secretion which soaks up the papillae of the stigma, a fundamental feature which has not been mentioned by any worker on these plants. The liquid is not oily as in many flowers but a clear, watery secretion. The function of such a stigma with unusual amounts of fluid is obvioulsy to liquefy dried pollen clots (see below) on the back of the pollinators and to 'sponge and brush' it off with the papillae as the pollinator crawls into, along and out of the circumambulator. Additionally, the stigmatic secretion dilutes and spreads the pollen over a wider area, reducing crowding of the huge masses of clumped pollen grains, thereby improving fertilization. This works also when pollinators carry fluid pollen mush.

Pollen

Unlike in most plants, the pollen grains in *Rafflesia, Rhizanthes* and *Sapria* are suspended in a fluid matrix. When attached to the anthers or freshly acquired, the pollen occurs as a mush with a consistency between mayonnaise and milk. In *Rhizanthes* it is paler and somewhat more fluid than in *Rafflesia* and *Sapria.* MEIJER (1958) and BEAMAN ET AL. (1988) assumed that for successful pollination, male and female flowers must be present at the same time so that pollinators can deliver pollen on the same day. However, BÄNZIGER (1991) proposed that calliphorids may deliver pollen weeks after they had acquired it.

It seems that nobody has been aware of some interesting features in the consistency and germinability of the pollen mush of the three genera: (1) once smeared off from the anthers it goes through a more or less fast coagulation, drying and hardening process depending on the humidity of the outside air; (2) the process is reversible under appropriate conditions; (3) the pollen retains its viability for an extended period of time even in the dry state.

In *S. himalayana,* under average early afternoon humidity and temperature in December–February (75–85 % RH, 16–18°C), the surface of a drop of mush on a microscope cover glass becomes covered with a dry film in 5–10 min. After 15–20 min the drop does not come off when gently wiped by dry fingers. An hour later the lower layers are also dry. In this state the clot has hardened and remains firmly stuck to the back of the pollinator lifelong unless it is liquefied again. In *Ra. kerrii* and *Ra. cantleyi* the pollen also clots but the speed of the process is not the same due to the different microclimate of their respective

Figure. 12. Large bud (14 cm circumference) and two small buds (left one 2.5 cm, right one 3.0 cm circumference) still enclosed in host tissue.

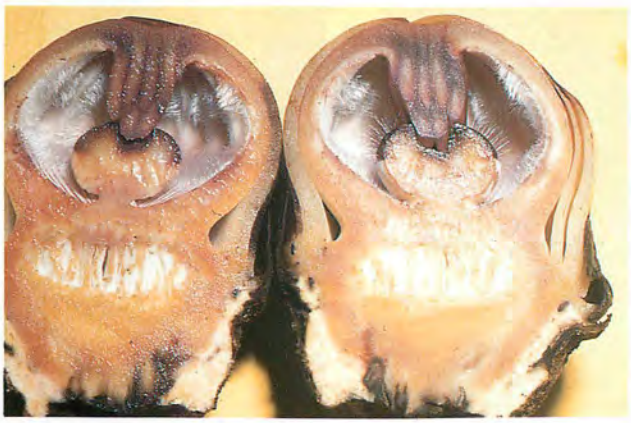

Figure. 13. Bud of 10.6 cm circumference cut to show white hairs.

Figure. 14. Fruit of *R. zippelii* (22 cm circumference).

Figure. 15. Trifoliolate leaves and ripe fruits of *Tetrastigma pedunculare.*

Figure. 16. Female inflorescence of *T. pedunculare.*

Figure. 17. Aerial roots of *T. pedunculare,* 1 cm diameter. Note the lenticels.

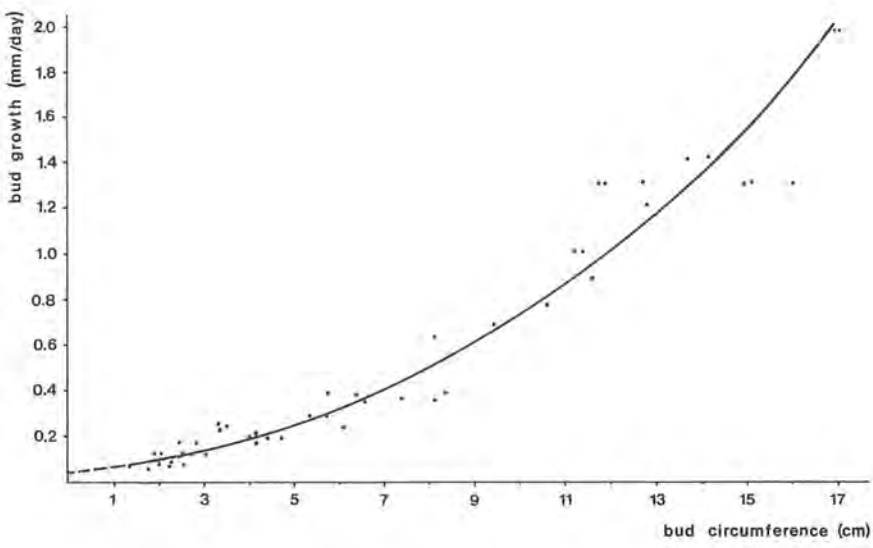

Figure 18. Relationship between bud size and bud growth rate of *R. zippelii* at site (a).

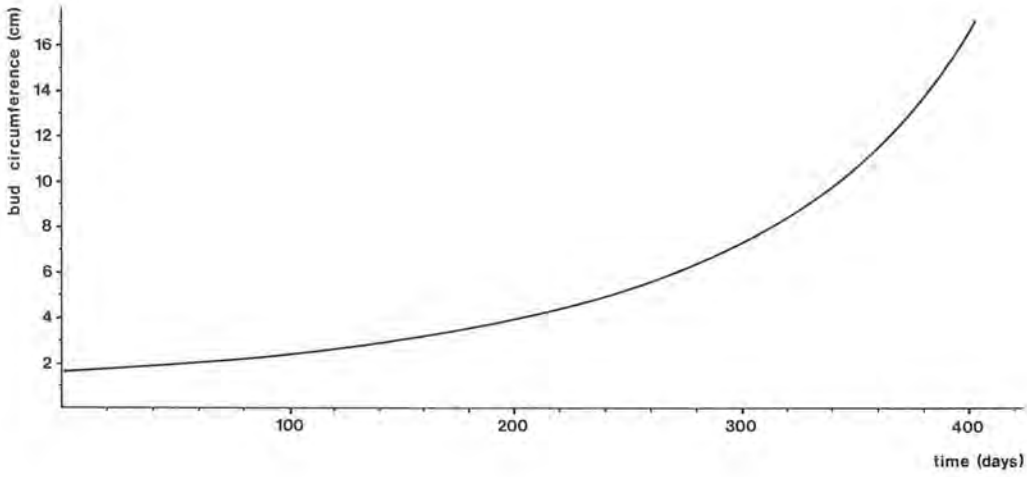

Figure 19. Average bud growth of *R. zippelii* based on growth rates derived from diagram 1.

habitats. *R. zippelii* occurs in a warmer and generally more humid habitat (22–30°C, 85–100% RH) than *S. himalayana* and its pollen mush becomes rubbery and not readily smearable in about 1 h, and hard in about 4 h. But the process is rather faster when wind from drier crest areas (e.g. 65 % RH) reaches the flower, or especially when exposed to strong air currents during the pollinators' fast flight, or when they bask in the sun or fly up into the canopy or other drier environments. Calliphorid fly pollinators were often caught with completely dry pollen smears, probably acquired in the previous day (s), both near *R. zippelii* and *Ra. kerrii.*

The process is reversible: addition of a drop of water or smear of stigmatic fluid to a clot dried on a slide or pollinator thorax liquefies the clot and floats the pollen grains in a matter of seconds.

Significantly, preliminary germination experiments show that the pollen of all four species retains substantial viability in the dry state for many days. Viability progressively declines over the next 3 weeks (no experiments yet made with *Ra. kerrii* pollen older than 11 days). This is much longer than pollen types carried by honey bees which generally last for less than a day (KRAAI, 1962; STANLEY & LINSKENS, 1974). Since conventional germination methods were not successful even with fresh pollen mush, pollen dried for specific periods of time, as well as fresh pollen, on splinters of cover slips was applied onto the stigma of live female rafflesiaceous flowers in the field, left for 24 h and then examined microscopically for pollen tubes. To prevent natural pollination, the flowers were covered with screening before opening. Germination of *R. zippelii* pollen occurred on the stigma of both *Sapria* and *Rafflesia;* germination was also successful across the latter two and among themselves. Experiments with the stigma of *R. zippelii* as germination medium could not yet be carried out. For several reasons (e.g. long distance transportation) the samples of pollen dried on cover slips could not be left at the site. It is possible that the different environmental conditions reduced the viability of the pollen.

The remarkable ability of the pollen of the three genera to solidify and be reliquefied by profuse stigmatic fluid has two important consequences. It ensures firm attachment of large pollen loads to the vector for long periods. It allows selective delivery, i.e. it is not lost on wrong stigmas when pollinators visit other flowers—as calliphorids often do—but can be sweapt off only by a fluid-soaked stigma. Virtually the only misdelivery which could occur is between *Rhizanthes* and *Rafflesia.*

In a number of individuals of *R. zippelii,* normal-looking anthers were exuding nothing but a colourless, clear fluid instead of the typical yellowish mush. Microscopic examination showed that such drops contained insignificant numbers of pollen grains. The drops dried as transparent clots and it is assumed that they are the matrix in which pollen grains are normally suspended.

In *R. zippelii* pollen mush conglomerates do not drop from the anther to the circumambulator to be sucked by pollinators, unlike what I had previously assumed to be the case with *Ra. kerrii* and *S. himalayana* (BÄNZIGER, 1991). Having seen many more of these flowers I now conclude that in *Ra. kerrii* pollen-dropping must be exceptional and in *S. himalayana* it might have been an artifact due to handling when cutting open the bud.

In *Mitrastemma yamamotoi* Makino the pollen is also suspended in a fluid matrix. However, in this species it is not water soluble but of lipidic base (WATANABE, 1936). Hence it is not affected by rain, unlike in *R. zippelii* where a single sustained shower will wash

off the pollen and destroy the flower's reproductive capability. In *Rafflesia* and *Sapria* the pollen is well protected, set below and off the margin of the disk, and also well above the base of the tube and thus it is not exposed to rain. In *M. yamamotoi* nothing is known about pollen clotting and its viability over time. However, it can be assumed that it does not clot, as is the case with the lady slipper orchid *Paphiopedilum villosum* (Lindley) Stein where the pollen matrix is also lipidic (BÄNZIGER, in press) and the pollen mass retains its very viscous consistency for many weeks. It is interesting to note that the pollen of this orchid retains its viability for at least 8 weeks while glued to the dorsum of its hoverfly pollinators, leading to normal capsule development when smeared onto the orchid's stigma (BÄNZIGER, in press).

Nectar

Another unexpected finding is the secretion of nectar (Fig. 3) on the pad covered by the ramenta. Prof. Dr. S. Vogel very kindly carried out histological analyses of the pads I had sent to him and confirmed that they contain nectar glands. The nectar appears in clear, colourless, initially more or less discrete droplets which merge and soak up the ramenta and sometimes part of the tuft hairs. It tasted sweet to my tongue and was sucked by a variety of insects ranging from the pollinating blow flies to non-pollinating visitors such as muscid and sarcophagid flies, honey and stingless bees, wasps, ants, butterflies etc. (BÄNZIGER, 1996). Since the nectar occurs near the margin of the lobes, hence far from where the actual pollination occurs, the nectar is functionally somewhat comparable to extrafloral nectaries; pollination is not a direct consequence of nectar uptake. This relocation may be an adaptation to ward off nectar thieves which might disrupt the activity of the true pollinators, and keep away from the flower's reproduction centre the most deleterious ants which devour nectariferous tissues.

The nectar was not present in all flowers. For instance, it was lacking in female 9.1 and male 5.8 and its absence was not due to depletion by insects (which can occur in a very short time), nor to ants (which can obliterate the tissue in a few hours). It is clearly an individual lack as observed in flowers kept under vigil from opening time. Absence of nectar in some flowers may indicate its reduced importance in the pollination process. Since pollinators are successfully lured to the circumambulator by other cues, nectar has lost to a wide extent its purpose.

Yet the nectar probably retains two minor functions. As a nourishment it 'wets' the appetite of the pollinators and induces them to remain on the flower, to crawl around and search for more, thereby increasing the chances of approaching the circumambulator. By offering a reward it induces calliphorids, which are capable of a certain degree of flower constancy (KUGLER, 1951), to visit another flower - important for pollen delivery onto a female.

Recently MEIJER *(in litt.)* also noted the presence of a secretion at the antler hairs.

Odours

CAMMERLOHER (1920) studied the stomata of *Rhizanthes* and *Rafflesia* and suggested that they are the places where the unpleasant odours are released. However, since they are

found exclusively on the underside (outside) of the perigone lobes they cannot be loci of odour emanation since this occurs on the upperside (inside). Also, insects attracted to the flower only settle on this side. Another function Cammerloher suggested is that they may release physiological water. However, because of the almost constantly high humidity of the microhabitat I do not think evaporation would be very efficient, nor have I seen droplets of water forming at the stomata.

MEIJER & VELDKAMP (1988) described the odour of *R. zippelii,* reported by various authors, as ranging from being virtually absent to being curiously acid, to foul and cadaverous. According to HEINRICHER (1905) the odour was not unpleasant and at any rate not carrion-like. Fresh flowers of my population emitted two very different, locally clearly separable odours, as assessed by close smelling. The stronger one originated from the tube, adjacent part of the lobe and possibly the column. I found it a most perplexing one and for want of a better description I would compare it to the stuffy air of a room with old furniture, and of a crowded room needing ventilation. The weaker odour emanated from the caudate appendages. It was rather more unpleasant and varied between cheesy to excrement-like. The odours were weak and generally perceptible only close to the flower but occasionally a faint whiff could be felt as far away as 1–1.5 m.

The odours are therefore quite different from that of *Ra. kerrii* (mostly rancid on perigone, variably fruity in the tube but cadaverous from some distance) and *Ra. cantleyi* (weaker in general, barely perceptible on the perigones, weakly reminiscent of foul eggs in the tube) (BÄNZIGER, 1991 and unpubl.). *S. himalayana* odour is also cadaverous but rather weaker than *Rafflesia's*.

To the human nose *R. zippelii's* odour was the weakest of the above but to flies it must be the most potent as shown in two experiments comparing *R. zippelii* and *Ra. cantleyi,* all four being normally visited by calliphorid flies before the experiments started. In both cases, one *R. zippelii* was cut an placed 50 cm from one *Ra. cantleyi* still *in situ.* In the first trial lasting 35 min *R. zippelii* was visited by 14 *Chrysomya pinguis* (Walker) and *C. chani* Kurahashi and *Ra. cantleyi* by only one *Hypopygiopsis infumata* (Bigot). In the second trial of 10 min, 18 *C. pinguis* and *C. chani* settled on *R. zippelii,* 6 on *Ra. cantleyi.* The calliphorids were not only more frequent but also more persistent on *R. zippelii* than on *Ra. cantleyi* though this could be additionally due to the former's perigone texture which mimics the fur of a mammal.

PHENOLOGICAL OBSERVATIONS ON *RHIZANTHES ZIPPELII*

Bud Growth

SOLMS-LAUBACH (1876) studied in great detail the anatomy and morphology of buds in various stages of development, from its inception on the thallus filaments of the parasite through to bud maturity, but its phenology has remained unknown. I monitored the growth of 101 buds from 31 March to 17 April in Thailand and of 63 buds from 16 to 31 January, 1995, in Malaysia. Size increments were measured as circumference at the bud's widest girth, but for practical reasons, in small buds this had to be obtained from measured diameters.

Buds first appear as small swellings which develop, still embedded in the brownish host tissue, into protruding, spherical nodules (Fig. 12). When about 3.7–4.1 cm in circumference they break through the host tissue. They remain enclosed in the fleshy and pale bracts (scales) until about 10 cm in circumference (about 2 months before flowering) when the actual bud starts to show below the receding tips of the bracts. The meridians - the brownish red lines along the fissures where the perigones split from each other - become increasingly evident, as does the bud coloration as a whole from its pale base to the brownish red top, while very slowly the bracts darken to eventually become dry, black and papery thin at least distally (Fig. 6, 12). Internally the buds have white hairs (Fig. 13) until about 11 cm in circumference. Their change to brownish has progressed about half way when about 12.5 cm and is completed when 13.5–14 cm in circumference (some 20 days before flowering) though parts of the nectar pads and antler hairs are still somewhat paler than the rest. From a circumference of about 13 cm onwards, it is possible to establish the sex of the bud from without. By gently bending down the bracts, one can see the shape of the walls of the neck. If it narrows downwardly, it is a male; if it widens or remains the same it is a female. The bud opens at an average circumference of 17.0 cm (min 14.7, max 20.5 cm) (16 buds measured within 12 hours before opening, except one measured 2 days prior to anthesis; its mature size was assessed by extrapolation).

The opening of a bud can be predicted within 1, sometimes 2 days, from the position of the last whorl of bracts, viz. its distinct divergence from the neck (Fig. 6), at least in males. In the female the divergence is not so obvious, probably due to the broader neck and its less inclined walls typical of females, which allow less space for divergence. Cracks along the meridians, formed first at the top of the bud long before anthesis, later widening and extending down the sides of the bud, are a further though only very approximate indication that in a number of days the bud will open. Furthermore, about two days before opening, bud expansion accellerates from 0.13–0.18 cm/day to 0.3–0.5 cm/day. An increased bud expansion rate shortly before anthesis is found also in other Rafflesiaceae. In *Ra. kerrii* in S Chumphorn Province the widening of three buds accellerated from a circumference increment of 1 cm/day to 3 cm/day 5 days prior to opening, leading to a maximum bud circumference of 75–85 cm (BÄNZIGER, unpubl.). Elliott (pers. comm.) found faster expansion also in the last bud stages of *S. himalayana.*

The growth rates of Thai and Malaysian populations correspond closely. From the curve (Diagram 2) it follows that when a bud breaks through the host tissue at a circumference of 3.7–4.1 cm, it needs some 200–225 days for flowering, but for the smallest measured buds of 1.6 cm circumference an estimated 400 days are needed. However, the data for the small buds are less reliable due to their slow growth and the short monitoring period. This is very close to the growth rates measured by ELLIOTT (1992) for *S. himalayana,* viz. 111 days from 7 cm circumference to flowering (105 days in *R. zippelii*). The giant *Ra. arnoldi* R. Brown needs nearly 500 days to grow from the circumference of 4.7 cm to flowering at 107 cm (MEIJER, 1958).

Anthesis

In Thailand the opening of four buds was followed throughout the night at hourly intervals. In three the perigones started to split apart around midnight, in the fourth around

0200 h, and this was completed around noon in all four. The other 17 buds (from all sites) were found flowering in the morning after being closed the previous afternoon; they also must have opened at night and the degree of flower expansion of the majority of them was within the same range. In three it was completed during 0900–1000 h. The final position of the recurved lobes varied from one just below the horizontal plane to a much more recurved position with the distal lobe parts more or less vertical and the caudate appendages horizontal instead of close to vertical as in the former. In the latter, which occurred in flowers not in direct contact with the ground, the expansion period lasted beyond noon.

The splitting apart started and was fastest on top of the bud where generally 3–4 wedge-like gaps formed (Fig. 7, 8) between groups of four or more perigones still attached to each other, together with their caudate appendages. The groups split into single perigones at various times later, though some only split partly or not at all. The tips of the caudate appendages, which generally were the last to separate, started to detach around 0300–0400 h when also the odour became more evident and the nectar droplets visible. By 0600-0700 h (Fig. 9) the caudate appendages were more or less horizontal and the lobes already overhanging, the whole giving the impression of a 'cage'. Around 0800 h (Fig. 10) the caudate appendages were inclined about 45°, resembling somewhat the spikes of a carnivorous plant ready to snap. By 0930–1030 h (Fig. 11) they were vertical and by noon they were open still more and the reflexing stopped or slowed down. As a comparison, *Ra. kerrii* needs about 24 h to open fully; 2 flowers started to open in the morning, one after night-fall (BÄNZIGER, unpubl.).

The best Thai cluster of *R. zippelii* had 3 flowers during 11 days, the best Malaysian had 7 during 9 days. One cluster in Thailand had 2 flowers which opened on the same day, both males. In Malaysia one cluster had 3 males and another cluster had a male and a female (deformed and incapable of reproduction) which flowered at the same time.

Flower Longevity

As already indicated by Bartel's notes (HEINRICHER, 1905), flower longevity is short. When no rain fell, the flowers looked 'fresh' for 2, at most 3 days and the odours were weaker and started to deteriorate on the second or third day, although flies still visited the flowers many days afterwards. After three days the odour was more mouldy.

Pollen depletion depends on the number of flies entering the circumambulator and their size and behaviour. I found that strong fly activity can exhaust pollen supply within a few hours and in all but one flower, pollen was depleted by mid-afternoon of the first day. Thus the chance of pollen washout by potential rain is not great since it is often already depleted by pollinators.

In the only female flower I was able to vigil from opening time, the stigma was wet during the first day, from early morning to evening. In another female, checked in the morning of its second flowering day, the stigma was slightly wet but it is not clear whether the liquid was stigmatic fluid or moisture due to rain or dew of the previous night. In yet another female, found when some three to five days old but still visited by flies, the stigma was dry. It is conceivable that females may be pollinated and fertilized on the second or few subsequent days with fresh pollen mush but not with dried pollen.

Rain also causes the tangle of furry hairs to collapse and stick to the perigone surface,

impairing the proper functioning of the pollination mechanism. Rain also causes a faster darkening and rotting of the fleshy parts of the flower which are then consumed by various nocturnal invertebrates, leaving only non-fleshy black tissue behind which can persist for many weeks.

Fruit

At all three sites there were very few remains of female flowers which might have been fertilized and developed fruit (Fig. 14). I left them *in situ,* but collected two for the study of the seeds. However, only one had what looked like not yet quite ripe seeds. They look very similar to *Rafflesia* seeds.

DISCUSSION

The populations of *Rhizanthes* of the three study sites, which doubtlessly belong to the same species, could not be identified unequivocally as either *zippelii* or *lowi* with the key of MEIJER & VELDKAMP (1988) nor by other descriptions of the two taxa. As there may not be enough justification for upholding two species and since *zippelii* BLUME (1827) has priority, I have opted for this name. Synonymization had been previously proposed by HOOKER (1873).

In an effort to resolve this problem I studied Beccari's descriptions of *lowi* in the original and also visited the well curated Herbarium Universitatis Florentinae. Unfortunately, the relevant type material is no longer there, and could not be traced. BECCARI'S (1868, 1869) *lowi* was not described from an open flower but from mere buds, and he could compare these only with the description and somewhat misleading illustrations of BLUME (1827). BECCARI'S description (1869) of *lowi* buds is detailed but his comparison with *zippelii* is somewhat confusing. He later (1875) reiterated his findings after studying *zippelii* material from the type locality and rejected HOOKER'S (1873) merger of the two species; this was followed by most botanists. Still, a description based only on buds, in a taxon lacking vegetative parts, is bound to be unreliable and problematic. Furthermore, much new information has accumulated during the intervening 120 years.

My view is that this *Rhizanthes* is highly variable. Like many parasites it has undergone reductions, a process which is probably still in progress as exemplified by the lack of nectar, or the secretion of pollen matrix without pollen, in some of the individuals. Reductions resulted in additional and possibly more evident new characters than in an ordinary plant. However, in *Rhizanthes* the characters used for the distinction of *zippelii* from *lowi* occur in various combinations and sometimes with transitions. In the past this was not sufficiently appreciated because of lack of material.

Probably the main feature which induced Beccari to think his species was different from *zippelii* is that according to BLUME (1827) this appears to be 5/6-lobed with bi- or tri-fissured caudate extensions. In reality the lobes and extensions simply did not separate completely into the normal 16 parts, the fissures being the lines along which the caudate extensions normally detach from each other.

The presence of tuft hairs in *lowi* and lack in *zippelii,* where Beccari says they are

replaced by the ramenta, does not seem to be reliable. The various types of hair formations are, as pointed out by HEINRICHER (1905) in his detailed studies of *zippelii,* rather variable. From various illustrations the tuft hairs appear to be less conspicuous but not entirely lacking and the ramenta merely somewhat more widely spread in some *zippelii.* Also, I have observed that the hairs are sometimes bitten off by ants, so that their absence may be an artifact of which previous authors were not aware. The number of *lowi's* anthers, 50–60, is not significantly outside the variation found in *zippelii* of 38–50 (31–52 in my populations). Beccari's mean deviation of ± 5 is suspiciously low (± 10.5 in my material), probably due to his very scanty study material. Beccari's other important distinction, viz. unisexual *lowi* and bisexual *zippelii,* turned out not to be consistent as shown by SOLMS-LAUBACH'S (1876) finding of pure males among the material from the type locality. HEINRICHER (1905) described even transitions with more or less strongly reduced organs of the opposite sex.

Also colour seems unreliable taxonomically. According to MEIJER & VELDKAMP (1988), *zippelii* has pale yellowish-white perigones and hairs at first bloom which soon turn to various shades of brownish red while *lowi* is so already before opening (MEIJER, *in litt.*). I consider these mere different physiological stages of the same colour development pattern. Buds at my sites had white hairs inside while smaller than 11 cm circumference but had brown ones when more than 14 cm. MOLESWORTH ALLEN (1968) described flowers of *lowi,* corrected to *zippelii* by MEIJER & VELDKAMP (1988), from near my populations as initially very pale pink, with white hairs before turning dark. HEINRICHER'S (1905) fresh *zippelii* from near the type locality had 'dirty white' perigones basally, fleshy coloured ones distally but pale caudate extensions, while the hairs were cinnamon. In a colour illustration (ANONYMOUS, 1995) *zippelii* from Sumatra has cinnamon as well as white hairs (difficult to see) on perigones which are bright white throughout except for the nectar pad with the ramenta and caudate extensions which are dark. MEIJER & VELDKAMP (1988) illustrated an 'aberrant' *lowi* where the basal half of the perigones and its hairs are white and the distal ones dark. In some of my buds (circumference 11–14 cm) the darkening occurred first on distal and basal perigone parts, the middle section remaining pale somewhat longer, while in others the nectar pads and ramenta stayed pale somewhat longer. To sum up, evidently the time and the area where parts of the flower turn from pale to brown are variable and occur in different combinations. In conclusion, it seems to me that, based on the data we have so far, there is no clearly defined, consistent character which separates *zippelii* from *lowi* and I would propose to merge the latter as a synonym into the former.

The relationship between *R. zippelii* and *T. pedunculare* is of particular interest, not so much because the liana is a new host and a new Thai record, but because of the parasite's restriction to a single host species over a wide area in Thailand and Malaysia. It was not found infecting any of the four other *Tetrastigma* and two non-vitaceous species reported as hosts by other authors. Significantly, among them was *T. tuberculatum* (my *Tetrastigma* sp. 12) which was growing at all sites and in some cases only a few meters from *R. zippelii.* At Malaysian sites 7 individuals (e.g. coll. No. 1205, 1206, 1232) were infected by clusters of *Ra. cantleyi. Tetrastigma hookeri* (e.g. coll. No. 1309, 1310, 1335) was also present at all three sites. In Thailand there was additionally *T. curtisii.* Neither though has been reported as host.

Yet, in spite of the finding of a new host it is well possible that future studies may

narrow down rather than widen the host range of *R. zippelii,* as happened in the case of *Rafflesia.* In Peninsular Malaysia, Latiff (pers. comm.) found that the hosts of *Ra. cantleyi* and *Ra. hasseltii* were all *T. tuberculatum* which is also the host for most other *Rafflesia* in Malaysian Borneo. I made corresponding observations. *Ra. cantleyi* at sites (b) and (c) are all on *Tetrastigma* sp. 12. North of the Isthmus of Khra, *Ra. kerrii* infects exclusively *T. quadrangulum* (16 clusters seen) but south of Khra to the Malaysian border, in a stretch of 600 km, I have found it parasitizing only *Tetrastigma* sp. 12 (15 clusters of six populations in four provinces (BÄNZIGER, unpubl.). I have checked the identity of *Ra. kerrii* hosts No. 086164 and 086168 (Forest Herbarium, Bangkok), mentioned as *T. papillosum* (NIYOMTHAM & KUBAT, 1987) and found them to be two different species, neither being *T. papillosum.* The actual host is *Tetrastigma* sp. 12 while 086164 is virtually certain to be *T. curtisii* which in S Thailand frequently occurs together with the actual host. Own field surveys in the area of 086164 and 086168 showed *Ra. kerrii* on *Tetrastigma* sp. 12, *T. curtisii* also being present but not infected. The two have similar stems and can easily be confused. Some *Tetrastigma* identifications in my paper (BÄNZIGER, 1991) are not flawless either (their primary identification though was not done by Prof. Latiff nor by myself): *T. lanceolarium* should be replaced by *T. hookeri.* There are some 57 *Tetrastigma* species recorded from Malesia (LATIFF, 1984), 16 from Thailand (CRAIB, 1926) and 39 from Indochina (GAGNEPAIN, 1912, 1930). A taxonomic revision of this difficult and still poorly known genus will likely synonymize many of them.

R. zippelii is a sapromyophilous flower since its pollinators are necro- and coprophagous Diptera, viz. mainly *Lucilia porphyrina* (Walker) and *C. pinguis* together with four further Calliphoridae besides an additional four as exceptional or potential pollinators. The syndrome is based mainly on brood-site deception as the carrion flies are deceived into laying hundreds of eggs, the hatchlings of which are doomed to starvation (BÄNZIGER, 1996). Thus the presence of a reward, viz. nectar, is somewhat unexpected because typically sapromyophylous flowers do not offer any. In fact, in the Rafflesiaceae there are only three other genera with species known to produce a sweet secretion. Their pollination syndrome is not definitively known, but evidence suggests that none is sapromyophilous. One is *Cytinus,* with *hypocistis* L. as the only European species of the family among several other elsewhere. The other is *Pilostyles,* richer in species and wider in distribution. *Cytinus hypocistis, P. thurberi* Gray and *P. hamiltonii* Gardner have floral nectaries lying at the base of the column (HAYEK, 1912; RUTHERFORD, 1970; DELL & BURBIDGE, 1981) which are therefore, unlike *R. zippelii,* directly involved in the pollination. An unidentified native wasp is the probable pollinator of *P. hamiltonii* (DELL & BURBIDGE, 1981) while a long-tongued hymenopteran is thought to pollinate *C. hypocistis* (HAYEK, 1912).

In the third genus, *Mitrastemma,* there is *yamamotoi* which produces large quantities of a sweet liquid which is exuded not by nectaries but through hydathodes as a guttation process (WATANABE, 1937). The hydathodes are located high on the column and the liquid collects mainly at the base of the perigones where it is taken up by such visitors as wasps, flies and a bird, *Zosterops palpebrosa.* WATANABE (1936) considered the insects as well as the bird to be pollinators but this was only inferred as no actual pollen acquisition or delivery was observed.

R. zippelii therefore is only a 'half-deceptive' sapromyophilous flower (*sensu* DAUMANN, 1971) which is an uncommon type, as found in some but by no means all *Aristolochia,*

such as *grandiflora* Swartz (CAMMERLOHER, 1923; HILJE, 1984).

ACKNOWLEDGMENTS

Thanks are due to Dr. W. Brockelman, Mahidol University, and Dr. S. Elliott, Chiang Mai University, for criticizing and improving the manuscript, to Mr. G. Linder, former librarian at the Swiss Federal Institute of Technology, Zürich, who was able to find most obscure references. I am particularly indebted to Prof. Dr. S. Vogel, Wien University, for his histological verification of the nectaries. Prof. Dr. A. Latiff, Universiti Kebangsaan Malaysia, Bangi, carried out the most important identifications of *Tetrastigma* spp. Arachnologist Dr. P. Schwendinger, Innsbruck University, had to muster exceptional patience with my seemingly unending observations at the Malaysian sites but his extensive soil seaving was duely rewarded with many spider novelties. M. Wong showed us site (b). The late Dr. T. Smitinand and Dr. T. Santisuk, both of the Forest Herbarium, Bangkok, commented on *R. zippelii* in Thailand and suggested places of botanical interest respectively. I am particularly grateful to Mr. P. Sukumalanand who generously let me use his computer facilities, and for his and my other Department colleagues' support of the project. Miss S. Panthi helped with the table layout. Dr. W. Meijer, University of Kentucky, gave valuable information about Rafflesiaceae. Prof. G. Moggi and Mr. G. Padovani kindly let me see the *Rhizanthes* material at the Herbarium Universitatis Florentinae, Florence, Italy. The National Research Council, Bangkok, extended research approvals (No. 125/35 and 39/38).

REFERENCES

ANONYMOUS, 1995. Rafflesiaceae, in: The World of Plants, part 40. *Asahi Shimbun*, 22 January, p 98–102.

BÄNZIGER, H. 1982. Fruit-piercing moths (Lep., Noctuidae) in Thailand: A general survey and some new perspectives. *Mitt. Schweiz. Ent. Ges* 55: 213–240.

BÄNZIGER, H. 1989. Lardizabalaceae: New plant family for Thailand 'predicted' by rare moth on Doi Suthep. *Nat. Hist. Bull. Siam Soc.* 37: 187–208.

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. 1996. Pollination of a flowering oddity: *Rhizanthes zippelii*(Blume) Spach (Rafflesiaceae). *Nat. Hist. Bull. Siam Soc.* (in press).

BÄNZIGER, H. (in press.). The mesmerizing wart: pollination ruse of epiphytic lady slipper orchid *Paphiopedilum villosum* (Lind.) Stein (Orchidaceae). *Bot. J. Linn. Soc.* No. 120.

BEAMAN, R. S., P. J. Decker AND J. H. Beaman. 1988. Pollination of rafflesia (Rafflesiaceae). Amer. J. Bot. 75: 1148–1162.

BECCARI, O. 1868. Descrizione di tre nuove specie di piante Bornensi. *Atti Soc. Ital. Sci. Nat.*11: 197–198.

BECCARI, O. 1869. Illustrazione di nuove specie di piante Bornensi. Rafflesiaceae. *Nuovo Giorn. Bot. Ital.*1: 84–91 (+ Table 5).

BECCARI, O. 1875. Osservazioni sopra alcune Rafflesiacee. *Nuovo Giorn. Bot. Ital.*7: 70–75.

BLUME, C. L. 1827. Over een nieuw Plantengeslacht, de Brugmansia, uit de natuurlijke familie der Rhizantheae. In H. C. van Hall, *Bijdr. Natuurk. Wetensch.* 2: 419–422.

CAMMERLOHER, H. 1920. Der Spaltöffnungsapparat von *Brugmansia* und *Rafflesia. Österr. bot. Zeitschr.* 69: 153–164.

CAMMERLOHER, H. 1923. Zur Biologie der Blüte von *Aristolochia grandiflora* Swartz. *Österr. bot. Zeitschr.* 72:

180-198 (+ Table 5–7).

CRAIB, W. G. 1926. *Florae Siamensis Enumeratio.* Siam Soc., Bangkok.

DAUMANN, E. 1971. Zum Problem der Täuschblumen. *Preslia (Praha)* 43: 304–317.

DELL, B. AND A. H. BURBIDGE. 1981. Notes on the biology of *Pilostyles* (Rafflesiaceae) in Western Australia. *West. Austral. Herb. Res. Notes* 5: 71–79.

DELPINO, F. 1868. Ulteriori osservazioni e considerazioni sulla Dicogamia nel regno vegetale. *Atti Soc. Ital. Sci. Nat.* 11: 265–332.

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

ELLIOTT, S. 1992. The status, ecology and conservation of *Sapria himalayana* Griff. (Rafflesiaceae) in Thailand. *J. Wildlife in Thailand* 2: 44–52.

GAGNEPAIN, F. 1912. *Flore générale de l'Indo-Chine.* Masson, Paris.

GAGNEPAIN, F. 1930. *Flore générale de l'Indo-Chine.* Supplément. Masson, Paris.

HANSEN, B. 1972a. Notes on some parasitic phanerogams from the Indo-Chinese Peninsula. *Bot. Tidsskr.* 67: 146–151.

HANSEN, B. 1972b. Rafflesiaceae. *Flora of Thailand,* 2: 182–184. Appl. Sci. Res. Corp. Thailand, Bangkok.

HAYEK, A. von. 1912. Über die Blütenbiologie von *Cytinus Hypocistis* L. *Österr. bot. Zeitschr.* 62: 238–240.

HEINRICHER, E. 1905. Beiträge zur Kenntnis der Rafflesiaceae. I. *Denkschr. K. Akad. Wiss. Wien, mathem.-naturw. Kl.* 78: 57–81 (3 Tables).

HILJE, L. 1984. Fenologia y ecologia floral de *Aristolochia grandiflora* Swartz (Aristolochiaceae) en Costa Rica. *Brenesia* 22: 1–44.

HOOKER, 1873. Reference in Heinricher, 1905.

HOSSEUS, C. C. 1907. Eine neue Rafflesiaceengattung aus Siam. *Bot. Jb.* 41: 55–61.

KUGLER, H. 1951. Blütenökologische Untersuchungen mit Goldfliegen (Lucilien). *Ber. Dtsch. Bot. Ges.* 64: 327–341.

KRAAI, A. 1962. How long do honey-bees carry germinable pollen on them? *Euphytica* 11: 53–56.

LATIFF, A. 1984. Studies in Malesian Vitaceae. VII. The genus *Tetrastigma* in the Malay Peninsula. *Gard. Bull. Sing.* 36: 213–228.

LATIFF, A. AND K. MAT-SALLEH. 1991. *Rafflesia.* In R. Kiew (ed.), *The state of nature conservation in Malaysia,* 89–94. Malayan Nature Society, Kuala Lumpur.

MEIJER, W. 1958. A contribution to the taxonomy and biology of *Rafflesia arnoldi* in West Sumatra. *Ann. Bogor.* 3: 33–44.

MEIJER, W. 1984. New species of *Rafflesia* (Rafflesiaceae). *Blumea* 30: 209–215.

MEIJER, W. AND J. F. VELDKAMP. 1988. A revision of *Rhizanthes* (Rafflesiaceae). Blumea 33: 329–342.

MOLESWORTH ALLEN, B. 1968. Interesting jungle plants. *Mal. Nat. J.* 21: 29–33.

PIJL, L. VAN DER. 1933. Korte mededeelingen. Mycetanthe (Brugmansia) Zippelii (Bl.) Hochr. *Trop. Natuur.* 22: 51–52.

NIYOMDHAM, C. AND R. KUBAT. 1987. Balanophoraceae and Rafflesiaceae of Thailand. *In* H. Weber and W. Forstreuter (eds.), *Parasitic Flowering Plants,* Proc. 4th ISPFP, Marburg.

RUTHERFORD, R. J. 1970. The anatomy and cytology of *Pilostyles thurberi* Gray (Rafflesiaceae). *Aliso* 7: 263–288.

SMITINAND, T. 1980. *Thai plant names.* Funny Publishing, Bangkok.

SOLMS-LAUBACH, H. GRAFEN ZU. 1874. Über den Bau der Samen in den Familien der Rafflesiaceae und Hydnoraceae. *Bot. Zeitung* 32: 337–342, 353–358, 369–374, 385-389 (+ Table 8).

SOLMS-LAUBACH, H. GRAFEN ZU. 1876. Die Entwicklung der Blüthe bei *Brugmansia Zippelii* Bl. und *Aristolochia Clematitis* L. *Bot. Zeitung* 34: 349–361, 365–370, 481–489, 497–503 (+ Table 8).

SOLMS-LAUBACH, H. GRAFEN ZU. 1898. Die Entwicklung des Ovulum und des Samens bei *Rafflesia* und *Brugmansia. Ann. Jard. Bot. Buitenzorg,* Suppl. 2: 11–21.

STANLEY, R G. AND H. F. LINSKENS. 1974. *Pollen: Biology, Biochemistry, Management.* Springer, Berlin.

TAKHTAJAN, A. L., N. R. MEYER AND V. N. KOSENKO. 1985. Pollen morphology and classification in *Rafflesiaceae* s.l. *Bot. Dzj.* 70: 153–162 (in Russian, English summary).

WATANABE, K. 1936. Morphologisch-biologische Studien über die Gattung *Mitrastemon.* I-IV. *J. Jap. Bot.* 12: 603–618, 698–711, 759–773, 848–858.

WATANABE, K. 1937. Morphologisch-biologische Studien über die Gattung *Mitrastemon.* V-VII. *J. Jap. Bot.* 13: 14–24, 75–86, 154–162.