BISEXUAL RHIZANTHES LOWII (BECCARI) HARMs (RAFFLESIAEACE) FROM BORNEO: FIRST DESCRIPTION OF FLOWERS, FRUITS AND SEEDS

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ABSTRACT

Rhizanthes lowii bisexuals differ from unisexuals mainly in column morphology. In bisexuals the column carries both the stigmatic fascia and, below it, the annular row of anthers, both being only about half the size of those found in unisexuals (column with either the stigma or the anthers). Sexually dimorphic characters (length of the caudal appendages, depth of the ampulla's crater and width of the stalk) are not intermediate in bisexuals but follow the female model, i.e. they are shorter, shallower and wider, respectively, than in males. When ripe the fruit is a blackish berry, 23–25 cm in circumference, 5 cm long, with tangential and vertical cracks on side walls, radial and circular cracks on the disk-like top. Seeds are minuscule, pitted, 0.70–0.78 mm long and 0.33–0.4 mm wide. An updated key for the identification of the four known species of Rhizanthes is presented, along with documentation by photographs and drawings, and biological notes.

Among Rafflesiaceae, bisexuals were known only in R. zippelii (Blume) Spach, a Javan species. R. lowii is Bornean and the finding of bisexuals in this species is additional evidence of R. zippelii's absence from Borneo; earlier reports of the latter's presence on Borneo are probably due to misidentification based on this peculiar character.

Key words: Borneo, bisexual, frugivores, fruit, Java, Rafflesiaceae, Rhizanthes lowii, Rhizanthes zippelii, seeds, unisexual.

INTRODUCTION

Rafflesiaceae are believed to have exclusively unisexual flowers except in one species, viz. Rhizanthes zippelii (Blume) Spach, which has both unisexual and bisexual flowers (Blume, 1827; Solms-Laubach, 1876, 1891; Heinricher, 1905; Meijer & Veldkamp, 1988; Meijer, 1997). The family is now generally considered to hold only three genera: Rafflesia with 13–22 species, Rhizanthes with 4 species, and Sapria with 3 species (Meijer, 1997; Bänziger & Hansen, 1997, 2000; Nais, 2001; Barcelona & Fernando, 2002; Latiff & Wong, 2003; Fernando & Ong, 2005; Barcelona, Cajano & Hadsall, 2006; Lays, 2006).

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Being in the shadow of its giant Rafflesia relatives, until recently, Rhizanthes has remained poorly known with its more modest flowers of often disconcerting aspect. In a first taxonomic revision of the genus (MEIJER & VELDKAMP, 1988), R. zippelii's distribution was extended from Java to Borneo, Sumatra and Peninsular Malaysia. We assume that Meijer was induced to extend its distribution to Borneo mainly by the presence there of some bisexual forms (then still thought to be exclusive to R. zippelii), while its extension to Sumatra was probably based on his finding there of some white specimens (white colour at that time being considered characteristic for R. zippelii). Its extension to Malaya was based on a population of Rhizanthes discovered by MOLESWORTH ALLEN (1968) which, although originally identified by her as R. lowii (Beccari) Harms, was later amended to R. zippelii (MEIJER & VELDKAMP, 1988). Unfortunately, in Molesworth Allen's specimens the colour was probably partly from aberrant flowers, partly from immature and old flowers. Because of all the above and other discrepancies, BÀNZIGER (1995, 1996) proposed to merge the two species [this had previously been suggested by HOOKER (1873)] and adopted R. zippelii, the older name, for the taxon he studied in South Thailand and West Malaysia. In the landmark treatment of the Rafflesiaceae by MEIJER (1997), the Malay taxon was reverted back to R. lowii.

In a second revision which included significant fresh material from the field as well as herbarium specimens (BÀNZIGER & HANSEN, 2000), R. zippelii was confined to Java, replaced in Sumatra by the new R. deceptor BÀNZIGER et Hansen, and replaced in the Malay Peninsula by the new R. infanticida BÀNZIGER et Hansen. The latter was also confirmed as far north as southernmost Thailand and West Sumatra. R. lowii, described from Borneo (BECCARI, 1868, 1869, 1875) but extended to Sumatra and the Malay Peninsula (MEIJER & VELDKAMP, 1988; MEIJER, 1997), was also restricted again to Borneo. A fifth taxon from North Sumatra, with ramenta reminiscent of R. lowii but with a white basal half as in R. deceptor in abrupt contrast to the brownish nectar pads, was excluded from the second taxonomic revision because it was incompletely known; it is likely to be a new species. The second revision closely followed Beccari, who in his original description of R. lowii pointed out the differences vis-à-vis R. zippelii, and HEINRICHER (1905) who underpinned him and made the most detailed study of R. zippelii so far.


During a recent visit to Sabah in northern Borneo, HB had the opportunity to study R. lowii: buds, flowers, fruits and, from left-overs of frugivorous rodents and scandents, the seeds. Observations were also made on its pollination and other reproductive aspects. However, arguably the most exciting result was that the flowers were bisexual, although it appears that this is not the first time bisexuality had been found in Rhizanthes on Borneo. MEIJER & VELDKAMP (1988) and MEIJER (1997) must have seen herbarium material of bisexual forms from the island but they allocated it to R. zippelii Similarly, a single bud from Borneo with typical R. lowii characters had been allocated to R. zippelii because it was bisexual (BARKMAN
Below we describe bisexual *R. lowii* for the first time. We hope that our study will dispel lingering doubts about the absence of *R. zippelii* on Borneo.

**MATERIALS AND METHODS**

Observations were carried out by HB on private land in Ulu Moyog, Penampang District, Sabah, East Malaysia, from 17 January until 5 February, 2006. The sites were in steep, dark gullies near streams in evergreen rain forest between about 400 to 1000 m a.s.l. The data presented here are from live specimens studied *in situ* with a powerful hand lens and a small angled dentist’s mirror to view recondite parts, and from photographic documentation, as well as from a limited amount of collected material. This was intentionally kept small so as not to impact the species. It mainly included moribund or dead flowers and buds, accidentally knocked off live buds by us or the villagers, cuts of small, not vital but taxonomically important parts of flowers, and remnants of pulp with seeds from fruits eaten by frugivores. They are deposited at the Sandakan Herbarium except two collections on long term loan via HB to the Bangkok Herbarium. No fruit was collected. All illustrations are by HB except the SEM micrographs (Figs. 16–18) made by standard procedures by AK.

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**Figures 1–6  *Rhizanthes lowii*  
(1) Cross-section of female flower; (2) male column; (3) frontal view of bisexual column (hairs omitted); (4) enlargements of variously shaped ramenta; (5) distal part of bristles; (6) tuft hairs. a, anthers; am, ampulla; br, bristles; ca, caudal appendage; cr, crater; rm, ramenta; sf, stigmatic fascia; st, stalk; th, tuft hairs. Figs. 1, 2 and 4–6 slightly modified after BANZIGER & HANSEN (2000).
RESULTS

Description of *R. lowii*

**Bisexual flowers (Figs. 1–12)**

We observed a total of five flowers (four found freshly opened in the morning thanks to careful monitoring of bud growth, one some two weeks old, black, well beyond anthesis), and about 20 buds in various growth stages. They grew in nine separate clusters from 50 m to a few km apart. All but two of the analyzed specimens (five open flowers and seven buds) matched *R. lowii* as described in Bänziger & Hansen (2000) except that they were bisexual. All other characters were within the mentioned range (some bristles and tuft hairs were slightly longer). The two exceptions were not bisexuals but typical male forms (cf. Fig. 2). No female form (cf. Fig. 1) was found. The hitherto unknown bisexual column (Figs. 3, 9, 10) is described below.

The general shape of the column is essentially the same as that of female unisexual *R. lowii*, i.e. typically clearly longer and with a higher globular head than in males. However, since the bisexual column has to accommodate both the stigmatic fascia and, below it, the annular row of anthers, the sexual parts are much smaller than in unisexuals. The anthers are about half the length and the stigma about half the width of those in unisexuals. The anthers are generally unilocular (only one pore for releasing fluid pollen matrix) instead of having two superimposed loculi as in unisexuals. Three other, minor (less clear and consistent) sexual characters, viz. the depth of the ampulla’s crater, the length of the caudal appendages and the width of the stalk, tend to be shallower, shorter and wider, respectively, than in male unisexuals but agree more with the female unisexuals.

**Column morphometry**

Column 19–21 mm high; stalk (= collum, style) 4–6 mm high and 9–10 mm wide; globular head 15 mm high; ampulla 6–8 mm high and 20–25 mm in diameter; crater aperture 7–11 mm and depth 11–14 mm; width of stigmatic fascia 4–6 mm; width of annular row of anthers 2–3 mm. Number of anthers (= number of radial lines) 50–65.

**Fruit (Figs. 13–15)**

Fruits of Rafflesiaceae have drawn little interest compared to their flowers, although they are of fundamental importance for conservation. The mature fruit and seeds of *Sapria himalayana* were described only recently (Bänziger, 2004), nearly 160 years after the flower’s discovery. In *Rhizanthes*, Heinricher (1905) described and figured a nearly mature fruit of *R. zippelii* and Bänziger (1995) an unripe one of *R. infanticida*.

A total of six fruits of *R. lowii* were seen. Two were probably only half way through their development to judging from their still relatively small size and absence of cracks, while one other was nearer maturity. Two mature fruits were checked for two weeks. At the end of this period one of them was found broken open, only the lower parts of the side walls remaining, with the pulp and seeds nearly completely eaten. Another fruit was found nearly completely consumed. The frugivore involved in one case was probably a tree shrew: tooth marks in the pulp consisted of four parallel lines, corresponding to the lower incisors; several species of tree
Figures 7–8 Bisexual *R. lowii*. (7) Freshly opened flower. Note the very long ramenta pads (pale brown), typical of *R. lowii*. (8) Detail of flower. Note the white stigmatic fascia and, only partly visible below the stigma, the anthers. The bristles at tepal vertex (center left) are sparsely set, typical for *R. lowii*. The fly is female *Hemipyrellia ligurriens*, the main pollinator (size: 10 mm long). Colour photographs by H. Bänziger.
Figures 9–11  Bisexual *R. lowii*. (9) Flower cut *in situ* because considered moribund since it stopped to open fully. Note the column stalk, ring of anthers, stigmatic fascia, and red ampulla. The very long pads of ramenta are typical. (10) Cross section of a large bud found dead. Note the ampulla discolored to dark brown, the stigma and anthers yellowish to brownish. (11) Ramenta pads magnified. Note the relatively long, strongly branched ramenta (best seen along the edges and tip).
Figures 12–15  Bisexual R. lowii. (12) Two buds; the one in the foreground is 5.4 cm in diameter and is about to open, as visible from the splitting tepal tips. (13) Mature fruit (diameter 7.3 cm). Note the circular and radial cracks on top of the fruit, and the tangential and vertical cracks on the side walls. (14) Fruit. Note the cracks on the side walls. (15) Remains of fruit shown in (14), ten days later, nearly completely eaten by a presumed giant rat (*Leopoldamys* or *Simdamys*). Note the double parallel lines caused by the rat’s incisor teeth; the dark granulation are the seeds.
Figures 16–18 Seeds of bisexual *R. lowii*. Whole seed before (16) and after (17) removal of the periclinal wall. Bar = 0.2 mm. (18) Detail of pit of seed. Bar = 0.03 mm. SEM micrographs by A. Kocyan.
shrews occur in Borneo. EMMONS, NAIS & BIUN (1991) have documented photographically
the tree shrew *Tupaia tana* and the squirrel *Callosciurus notatus* eating the fruit of *Rafflesia
keithii* Meijer. From the remains of the second fruit of *R. lowii*, a rodent was involved since
the tooth-marks consisted of two parallel lines. They were 6.5 mm wide, hence far too large
for any other squirrel except giant squirrels (*Ratufa* spp.) which, however, live in the high
canopy. Tooth-marks which HB saw of *Callosciurus*-sized squirrels are in the region of 3–4
mm width only. HB suspects giant rats, either *Leopoldamys* or *Sundamys*, were the consumers. Jungle rats have previously been suspected and recently been proved to consume fruits
of *S. himalayana* in North Thailand (BANZIGER, 2004 and in prep.).

The mature fruit is a blackish berry comparable to that of *S. himalayana*. However, in
*R. lowii* it is not barrel-shaped but has side walls slightly converging towards the disk-like
top. It is also slightly smaller: 23–25 cm in circumference at the bottom and 3–5 cm in length
(from bract attachment to tepal attachment; 7 cm if measured from root attachment to tepal
attachment). Remnants of the bases of bracts, tepals and the stalk of the column remain.
As in *S. himalayana*, at a later development stage there are brownish cracks all over, circular
and radial on top, vertical and tangential on the side walls. They increase in depth and width
and at full maturity the fruit splits open along them exposing the white pulp and myriad of
tiny seeds. The wall thickness is about 7 mm.

**Seeds (Figs. 15–18)**

As already noted by BOUMAN & MEIJER (1994), the seeds of *Rafflesia* and *Rhizanthes*
are structurally essentially the same. The seeds of *Sapria* are also similar (BANZIGER, 2004).
Minor differences include the size of the seed (about a third longer in *Rafflesia kerrii*
compared to *S. himalayana*) and the number of pits in the exotegmen (slightly fewer but larger in
*Ra. kerrii*). Seeds of *R. lowii* are intermediate between *Rafflesia* and *Sapria* in length and pit
size. In *R. lowii* the seeds are 0.70–0.78 mm long (micropylar portion 0.36–0.44 mm, raphal
portion 0.29–0.36 mm) and 0.33–0.40 mm wide. The ultrastructure of the pits consisting of
small perforations (Fig. 18) is found also in *Sapria himalayana* and *Rafflesia kerrii*.

It has been demonstrated in experiments with rats (*Rattus norvegicus*) feeding on fruit of
*S. himalayana*, that seeds recovered from their dung had the periclinal wall removed after
gut passage (BANZIGER, 2004). It is well-known that in the seeds of many plants the periclinal
membrane must be removed (cf. Fig. 17) before germination can start but whether this is also
the case for Rafflesiaceae is not yet known.

Because of taxonomic changes since 2000, the seeds described by BOUMAN & MEIJER
(1994) as being of *R. lowii* and *R. zippelii* actually pertain to an incompletely known taxon
from North Sumatra and to *R. deceptor*, respectively (cf. Table 2 in BANZIGER, 2004).

**Additional notes on biology**

Hosts infected were *Tetrastigma pedunculare* (Wall. ex Laws.) Planchon (Vitaceae) at
low elevations but *T. papillosum* (Blume) Planchon at high elevations; the two host species
meet at around 600 m. The pollination will be treated in detail elsewhere but it is clear that
blow flies (*Calliphoridae*), especially *Hemipyrellia ligurriens* (Wiedemann) (Fig. 8), are
involved. The pollination system is sapromyiophily, but not of the pernicious type found in
*R. infanticida*. It is akin to that observed in *R. deceptor* where pollinators are not misled into
laying eggs (BANZIGER, 2001).
New Key to the Four Recognized Species

1a. A tangle of fine, strongly sinuous, intertwined, densely set furry hairs (600–1400 hairs/cm$^2$ at tepal vertex) covers most of the tepal; distally a short (3–14 mm) pad of ramenta may or may not be present. Radial lines 36–51. Tepal length 50–100 mm

2a. Ramenta absent. Basal 1/2–2/3 of tepal, and caudal appendage, ivory colour, distally 1/3–1/2 pale fleshy, ampulla dark brown. Unisexual or bisexual. W Java.......................... R. zippelii

2b. Non- to multi-branched ramenta cover distal 1/20–1/5 of tepal. Tepal pale yellowish basally, more centrally and distally a tendency to pale brownish with grayish-pink tone, overshadowed by cinnamon hairs; tuft hairs and pad with ramenta dark brown; caudal appendages and ampulla pinkish brown. Unisexual only. S Thailand, W Malaysia and Sumatra.......................... R. infanticida

1b. Relatively stiff, not so sinuous, sparsely set bristles (20–70 bristles/cm$^2$ at tepal vertex), cover much of the tepal; distally a short to very long (7–90 mm) pad of ramenta. Radial lines 46–70. Tepal length 75–135 mm

3a. A pad of non- to moderately-branched ramenta covers distal 1/15–1/5 of tepal which is 75–100 mm long. Radial lines 46–54. Tepal white throughout except near the apex where there is a dark brown area with tuft hairs and ramenta. Unisexual only. Sumatra.......................... R. deceptor

3b. A pad of strongly multi-branched ramenta covers distal 1/3–2/3 of tepal which is 90–135 mm long. Radial lines 50–70. Tepal pale yellowish basally, but centrally and distally gradually darker to brownish, with or without reddish brown areas, whitish to yellowish speckles or marbling; area of ramenta cinnamon to brown. Unisexual or bisexual. Borneo.......................... R. lowii

Emendation

In Bänziger & Hansen (2000), in the description of R. lowii, R. infanticida and R. deceptor, under section ‘Colour’ on pp. 126, 128 and 131, respectively, the term ‘column’ should be replaced by ‘collum’, i.e. the stalk (in females the style, see Fig. 2 there) which supports the globular head. Further, in the section ‘Description’ on the same pages, ‘style’ should be replaced by ‘collum’ because the term style applies only to females. Finally, in R. deceptor the collum is reddish rather than pale yellowish.

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