

A NEW TAXONOMIC REVISION OF A DECEPTIVE FLOWER, *RHIZANTHES* DUMORTIER (RAFFLESIIACEAE)

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ABSTRACT

Re-evaluation and recombination of old and new characters obtained from extensive field and herbarium research, show that the two hitherto known, not reliably separable species of *Rhizanthès* actually consist of at least four species: *zippelii* (Blume) Spach from Java, *lowii* (Beccari) Harms from Borneo, *deceptor* sp. n. from Sumatra, and *infanticida* sp. n. from South Thailand, West Malaysia and Sumatra. All are described, illustrated, keyed, and provided with data on habitat, parasitized hosts and pollination.

INTRODUCTION

Flowers of the parasitic genus *Rhizanthès* Dumortier 1829 are deceptive in more than one way. Their medusa-like appearance, hairiness, colour, odour and exudations elicit very contrasting behaviours in visitors. For pollinating carrion flies they dissimulate a corpse on which they are tricked into laying ill-fated eggs; for bees, wasps, ants, and butterflies they are a place to steal nectar; to certain male flies they are a vantage ground to lurk for females; to biologists, a source of frequent disagreement.

In the first taxonomic revision MEIJER & VELDKAMP (1988) comprehensively summarized what was then known of *Rhizanthès*. New biological and ecological data, including pollination, as well as details of the parasitized lianas, were given by BÄNZIGER (1995, 1996).

MEIJER & VELDKAMP's (1988) taxonomic circumscription and identification key for the two known species, *R. zippelii* (Blume) Spach and *R. lowii* (Beccari) Harms, were later reassessed by MEIJER (1997). Unfortunately, neither treatment is reliable. For instance, one of the main characters for species distinction was strongly branched ramenta in his *lowii* and once or twice branched ramenta in his *zippelii*, but the Thai–Malayan taxon, which he corrected to *zippelii* and back to *lowii*, has variably non- to multi-branched ramenta, while *zippelii* from the type locality in Java lacks the ramenta altogether.

In fairness, a revision of such a rare, morphologically reduced parasite is an arduous and tricky undertaking since crucial old material has not preserved well, or is lost; field notes on colour, made by various authors, are generally inadequate and often contradicting, and the original collecting localities are now mostly destroyed.

Nevertheless, one problem is Meijer's over-emphasis on one particular character, the shape of the tip of the antler hairs or ramenta. Unfortunately, the ramenta can be extremely

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variable and, as pointed out by MEIJER & ELLIOTT (1990) in a study of *Rafflesia kerrii* Meijer, the ramenta and the white dots on the diaphragma are derived from the same structures and represent extreme variations of them. Such variable structures need careful evaluation and their significance put in proper relation to other characters. For instance, other hair formations, such as the furry hairs and the bristles (e.g. Figs. 13, 18), are fundamental and readily recognizable characters even by the naked eye.

The other major problem is the colour *in vivo*. While this may vary, as in other Rafflesiaceae, due to age and external factors such as weather, a feature particular to *Rhizanthus* may have led to discrepant colour assessments: densely hairy taxa tend to be assessed according to hair colour (generally brownish), and sparsely hairy ones according to colour of the surface on which the hairs are set (generally white to yellowish to brownish).

Furthermore, perhaps induced by notes from Bartel (in HEINRICHER, 1905) and WINCKEL (1918), MEIJER & VELDKAMP (1988) stated that after the initial brief white stage, the flowers always turn to various shades of red and brown. This led BÄNZIGER (1995) to assume that the colour difference between white *zippelii* and brown *lowii* is due to differing development stages and therefore not taxonomically significant, especially since he found that buds, up to a relatively late stage, are white inside also in the brown-flowering taxon. In reality, the white colour was recently discovered to be consistent throughout the flowering period in W Sumatran flowers (pers. observation by HB), requiring a thorough re-evaluation of this character.

It is not surprising, therefore, that HOOKER (1873) sank *lowii* into a variety of *zippelii* although this was not widely adopted. In order to identify Thai–Malayan *Rhizanthus*, BÄNZIGER (1995) carried out a detailed analysis of the characters used in various publications for separating the two species. No one had yet mentioned the striking difference between the furry hairs and the bristles, and identification proved impossible. He concluded that the characters occur in various combinations and sometimes with transitions and proposed that the two species be merged. Since *zippelii* had priority, and because MEIJER & VELDKAMP (1988) had re-identified the taxon from the same area in Malaysia as *zippelii*, BÄNZIGER (1995, 1996) opted for this name.

One of us (HB) carried out new field research in all main distribution areas of *Rhizanthus*, viz. the Thai–Malay Peninsula, the islands of Sumatra, Java and Borneo. Unfortunately, none were found in Java where, according to MEIJER (1997), no sightings have been made since 1940. HB also studied the *Rhizanthus* material preserved in the Herbarium Bogoriense (BO), Brunei Forestry Center (BFC), Andalas University (AU) (Padang, Sumatra), and Universities of Innsbruck (UI) and Zürich (UZ), while BH did so with material from Leiden (L).

As a result, by critically re-evaluating and recombining old and new characters, and comparing the geographical distribution, four character groups have been found, one each in Borneo and Java, and two in Sumatra, one of which is shared with the Malay Peninsula. A fifth group, from Sumatra, is incompletely known and is thus excluded from taxonomic recognition at this stage.

The four groups can be neatly distinguished, but the differences between them are relatively small—only hairiness, colour, size of flower, and minor differences in column structure, etc. This, and slightly overlapping characters in a few specimens—the status of their preservation does not allow us to be sure—would indicate that *Rhizanthus* is best regarded as having a single species with several infraspecific taxa.

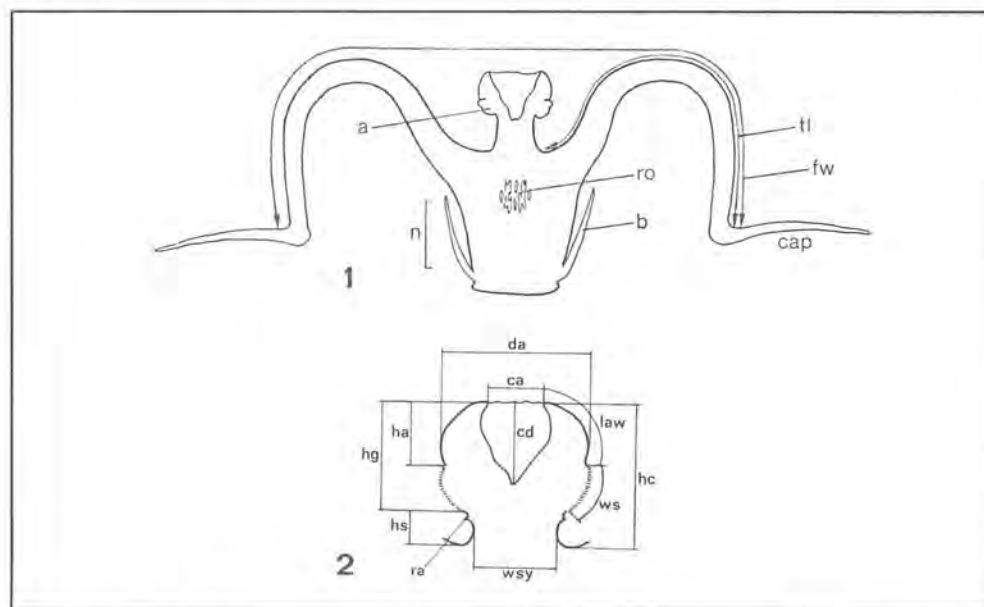
Nevertheless, many authors, beginning with Beccari and Heinricher, attach fundamental significance to such characters and probably would not have hesitated to recognize all four taxa at species rank. The new taxa certainly differ among themselves, and from the already known ones, as much as the latter do from each other. Since by upholding *lowii* at specific rank we contribute to nomenclatural stability, and because binomials are given far more importance than trinomials, and finally because rare species have greater chances of being protected than rare subspecies, we rank all taxa at species level. We hope that our findings will stimulate further research to establish their proper rank.

MATERIALS, METHODS AND TERMINOLOGY

For better preservation the HEINRICHER (1905) method was used (brief boiling in alcohol to reduce subsequent blackening of the specimens). Pros and cons of this method, and the finding that ethanol preservation (60–70%, with or without boiling) causes a slight shrinking of 5–12% compared to specimens *in vivo*, will be published elsewhere.

Size measurements were taken as explained in Figs. 1–2 and are based on alcohol preserved specimens (except where otherwise mentioned). As pointed out above, these are slightly smaller than live specimens. Circumference of buds was measured at maximum width.

All illustrations are by HB except Figs. 27–29 which are from photographs by A. Kocyan.



Figures 1–2. Morphological terms and measurements. Cross-section of male flower (1) and of female column (2). a=anther, b=bract, cap=caudal appendage, ca=crater aperture, cd=crater depth, da=diameter of ampulla, fw=flower width, ha=height of ampulla, hc=height of column, hg=height of globular head, hs=height of style, law=length of ampulla wall, n=neck, ra=reduced anther, ro=reduced ovary, tl=tepala length, wsy=width of style, ws=width of stigmatic fascia.

GENERAL MORPHOLOGY

The number of tepals is typically 16 (rarely 14–15) but this is not always evident because sometimes two or more tepals remain fused. Also, the longitudinal extent of separation varies from tepal to tepal, though they mostly detach from each other about 1/3–1/2 of their length from the apex. Thus, unlike in *Rafflesia* and *Sapria*, in *Rhizanthus* the size of the perigone lobes is not a stable character and is not used in our morphometric analysis. We use tepal length instead (measured as shown in Fig. 1). The basal, fused part of the tepals forms a campanulate tube and, most internally around the column, the circumambulator.

The radial lines (Fig. 22) are shallow furrows which are always darker than the basal part of the tepals in all taxa and therefore readily apparent throughout anthesis (the first 3 days after the bud opens around midnight). More distally they fade and/or the wall becomes darker so that they are no more evident. Internally they can be followed up the column (much less evident in females) to the base of the anthers, to which they correspond in number, even in unisexual females which always have a tiny row of reduced anthers (often partially merged into a crest) at the lower edge of the stigma (Fig. 2). The correspondence between radial lines and anthers, the number of which varies appreciably within a certain limit typical for each species, is very useful because the lines are always readily evident and thus a practical indication of the number of anthers, even in females. The shallow ridges between the dark furrows correspond to the strongly produced tube ridges in *Sapria* Griffith which, however, invariably have 20 ridges and anthers, or strongly reduced anthers in females, in all three known species (BÄNZIGER & HANSEN, 1997).

The ovary is inferior and consists of irregular cavities, bearing great numbers of ovules. As in *Sapria*, the ovary is present also in male *Rhizanthus* albeit likewise reduced. It is contained in the neck, the basal section of the flower connecting to the cupula (the attachment of flower to host), and is important for the *in vivo* distinction of the sex of the flower while still in the bud stage (BÄNZIGER, 1995): In the female the neck is narrowest below the perigone insertion and widest further down, where the main body of the ovary is (Fig. 17). Hence the walls of the neck converge upwardly (rarely parallel). In males, due to the rudimentary ovary, the walls converge downwardly, the neck being narrowest where the last whorl of scales is attached (Fig. 13).

BÄNZIGER (1995) described morphologically and functionally four types of hairs in his Thai–Malayan taxon. Three are taxonomically relevant and redescribed here, together with an additional type, the bristles, not mentioned in *loc. cit.* because they are lacking in that taxon.

Furry hairs: 6–8 mm (sometimes up to 11 mm) long, fine and pliable (i.e. not stiff as the bristles) due to their comparatively small diameter of 0.02–0.05 mm at mid-length and relatively thin walls of 0.001–0.0035 mm. They are densely set, 600–1400 hairs per cm² near the vertex of the reflexed tepal (400–1700 hairs per cm² opposite the globular head), strongly sinuous, mutually intertwining in a 2–5 mm thick, woolly, mat-like tangle (Fig. 24). Cinnamon in colour, their apices are sometimes unbranched but generally hooked, slightly branched, sometimes strongly so. They are found only in *R. zippelii* and *R. infanticida* where they cover the tepals throughout except distally where they merge with the tuft hairs.

Bristles: 7–11 mm long, relatively stiff compared to the furry hairs due to a larger diameter of 0.04–0.09 mm at mid-length and thicker walls of 0.002–0.007 mm. They are

sparsely set (Fig. 26), 20–70 bristles per cm² near the vertex of the reflexed tepal (150–200 opposite the globular head). They are not, or only a little, sinuous, more or less standing upright and not forming a woolly, mat-like tangle but giving the flower a hispid appearance. Cinnamon to brown in colour, their apices are unbranched to slightly branched. They are found only in *R. lowii* and *R. deceptor* where they replace the furry hairs. Although morphologically similar to the tuft hairs, the bristles differ in their location and sparse distribution.

Tuft hairs: 6–12 mm long, somewhat stiffer yet with a diameter of 0.03–0.1 mm at mid-length and a wall thickness of 0.003–0.01 mm. They are moderately to very densely set with 450 to more than 2500 hairs per cm² and stand more or less straight or very slightly sinuous, upwards and sideways, in a dark brown tuft (Fig. 23) between the furry hairs/bristles and the ramenta, often partly soaked with nectar. Their apices are generally unbranched.

Antler hairs or ramenta (Fig. 23): short (0.3–2 mm), relatively thick (0.03–0.1 mm), very densely set (up to 15,000 per cm²), with unbranched to very strongly multi-branched apices. They tend to be shorter and less branched distally on the tepal, longer and more branched proximally. They are brown to very dark brown in colour and found distal to the tuft hairs on a nectariferous pad, soaked with nectar in fresh bloom. Depending on the taxon, they can be very widely to very narrowly distributed, or be completely absent.

Persistence of the White Colour in *R. deceptor* (Figs. 25, 32)

Bud development, anthesis, pollination, and morphology of a population of several clusters were studied in the field during 10 days in Ulu Gadut, W Sumatra. The white colour of 3 flowers found freshly opened in the morning (still buds of 225, 210, 200 mm circumference the previous late afternoon) was unchanged when one was collected in the afternoon of the first day, and two in the afternoon of the third day of anthesis. One of the flowers was kept sheltered by a large plastic basin to prevent damage from rain and debris. Barely any difference in whiteness was observed between the sheltered and unsheltered flowers on the third day. Also, despite rain, the bristles were still in position, unlike in *R. infanticida* where the tangle of furry hairs collapses in rain, causing a mess. However, an overall impression of deterioration seemed to have occurred in the unsheltered flower: insects had gnawed brownish holes in the white tepals; flies and other insects deposited dark faeces; dust and debris from the canopy accumulated on the wall or bristles, as did soil particles due to splashing rain, while ants bit off part of the nectariferous pads. This impression of deterioration, added in *R. zippelii* by the mess of collapsed furry hairs following rain, probably explains, at least in part, the misconception of the white colour's impermanence in the species.

DESCRIPTIONS

Rhizanthès

Rhizanthès Dumortier, Anal. Fam. Pl. 14 (1829); *Brugmansia* auct. non Persoon: Blume in Van Hall, Bijdr. Natuurk. Wetensch. 2: 422 (1827); *Zippelia* auct. non Blume: Reichenbach, Handb. Nat. Pfl.-Syst. 164 (1837); *Mycetanthè* Reichenbach, Deut. Bot.

Herb.-Buch 61 (1841) (unnecessary replacement).

Etymology. A composite word from Greek, *rhiza* (root), *anthos* (flower, gender neuter) or *anthes* (flowering), hence root-flowering, alluding to the site where flowers develop (not always correct). The gender would seem to be neuter but Dr. D. Nicolson (*in litt.*) pointed out that according to Art. 62.4 of the International Code of Botanical Nomenclature, generic names ending in *-anthes* are to be treated as feminine.

Buds ovoid-pyriform, when young pale, at maturity the upper half with brownish red meridians along the tepal margins and the top more or less brownish throughout. The 16 tepals valvate, basally encircled by 3–4 whorls of 5 ovate scales, dark brown at maturity. Flower with campanulate tube, radially striped, perigone lobes of variable length, tepals covered either with furry hairs or bristles, distally of these a tuft of straight hairs, followed by a patch of ramenta, which may spread as wide as the whole distal 2/3 of the tepal or lack completely. Tepal apex geniculate, with long caudal appendage (distal part of which sunk into the ampulla cavity when in bud stage). Central column with globular head, formed by hairy, brownish to pinkish brown ampulla above a papillose stigmatic fascia below which is, in bisexual flowers, the ring of anthers. In unisexual flowers, females with rudimentary anthers more or less merged in a tiny row, males with fully developed, 36–70 anthers with two superimposed loculi and a reduced ovary. Males differ from females in the smaller globular head, longer but narrower style, longer caudal appendages, deeper crater depth, narrower neck. Fruit globose, at maturity blackish, with traces of attachments of column, tepals, scales. Parasitic on a few *Tetrastigma* (Vitaceae) species.

Key to the Four Recognized Species

1. A tangle of fine, strongly sinuous, intertwined, densely set furry hairs (600–1400 hairs/cm² 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. Unisexual or bisexual. Tepal length 50–100 mm
2. Ramenta absent. Unisexual or bisexual. Basal 1/2–2/3 of tepal, and caudal appendage, ivory colour, distal 1/3–1/2 pale fleshy, ampulla dark brown. W Java
 1. *R. zippelii*
2. Non- to multi-branched ramenta cover distal 1/20–1/5 of tepal. Unisexual. Tepal pale yellowish basally, more centrally and distally tendency to pale brownish with greyish-pink tone, overshadowed by cinnamon hairs; tuft hairs and pad with ramenta dark brown; caudal appendages and ampulla pinkish brown. S Thailand, W Malaysia and Sumatra
 3. *R. infanticida*
1. Relatively stiff, not so sinuous, sparsely set bristles (20–70 bristles/cm² at tepal vertex), cover much of the tepal; distally a short to very long (7–90 mm) pad of ramenta. Radial lines 46–70. Unisexual only. Tepal length 75–135 mm
3. Non- to moderately-branched ramenta cover 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 dark brown area with tuft hairs and ramenta. Sumatra
 4. *R. deceptor*
3. Strongly multi-branched ramenta cover 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 brown. Borneo

2. *R. lowii*

A fifth, incompletely known, taxon from Sumatra has ramenta reminiscent of *lowii* but is white on the basal half of the tepal as in *deceptor* and *zippelii*, while the distal 1/2 of the tepal is brownish in abrupt contrast to the basal half.

1. *Rhizanthès zippelii* (Blume) Spach

Hist. Nat. Veg. 10: 554 (1841). *Brugmansia zippelii* Blume in Van Hall, Bijdr. Natuurk. Wetensch. 2: 422 (1827).

Figs. 3–7, 34–37, Appendix 1.

Description. Bud circumference at anthesis 150–210 mm. Flower bisexual or unisexual. Tepal 50–100 mm long, 8–17 mm wide, caudal appendages 15–57 mm long, total span of flower (incl. caud. app.) 158–290 mm. Except distally, tepal covered by furry hairs which densely set (800–1000 hairs per cm² near the vertex of the curved tepal, 1100–1700 per cm² opposite the globular head), 6–7 mm long, pliable (0.02–0.03 mm in diameter at mid-length and 0.001–0.002 mm wall thickness), mostly with pointed or faintly to clearly hooked, sometimes once- to multi-branched endings. Near the tepal apex, tuft hairs of similar length but 0.03–0.04 mm in diameter at mid length and 0.003–0.005 mm wall thickness, very densely set (over 2500 hairs per cm²). There are no ramenta.

Column 13–19 mm high; style 5–7 mm high and 11.5–13.5 mm wide in bisexuals, 3 mm high and 10 mm wide in females, 5–9 mm high and 8–10 mm wide in males; globular head 11–12 mm high in bisexuals, 13 mm in females and 7–10 mm in males. Ampulla wall 5–7 mm long in bisexuals, 9 mm in females and 5–7 mm in males; ampulla diameter 16–23 mm in bisexuals, 21.5 mm in females and 15–18 mm in males; its crater aperture 9.5–14 mm in bisexuals, 10.5 mm in females and 9–10 mm in males; its crater depth 6.5–8 mm in bisexuals, 7 mm in females and 12–18 mm in males. Width of stigmatic fascia 4–6.5 mm in bisexuals, 6.5 in females; annular row of anthers 2–4 mm in bisexuals and 4 mm in males. Number of anthers (=number of radial lines) 44–48 in bisexuals and 42–54 in males.

Colour (*fide* HEINRICHER, 1905). Basal 1/2–2/3 of tepal ivory, distal 1/3–1/2 pale fleshy, caudal appendages yellowish white, ivory, hairs cinnamon, column yellowish white, ampulla dark brown. Cf. remarks about discrepancies in colour noted by various authors.

Diagnosis. See key. Additional differences: with 11–13 mm bisexuals tend to have the smallest height of the globular head (15.5 mm in *lowii*, 14–16 mm in *infanticida*, 13–17 mm in *deceptor*), the flattest ampulla and widest style considering its size. The ampulla is stated to be dark brown, not reddish brown as in the other species.

Biology. Habitat: tropical rain forests at mid-elevations, 500–1100 m. Host: almost certainly *Tetrastigma papillosum* (Blume) Planchon, still present at the type locality (MEIJER, 1997, and pers. obs. HB). *T. pedunculare* (Wall. ex Laws.) Planchon, the host most commonly found parasitized by other *Rhizanthès* spp. elsewhere, has never been reported from Java.

Distribution. West Java.

Remarks. The flower colour mentioned by various authors is rather confusing; the real colour cannot be ascertained since no living botanist appears to have seen a fresh flower. HEINRICHER (1905) noted that, unless the reproduction of the illustration of the

hand-coloured edition of Blume (1827; we have seen the uncoloured edition only) was unnatural, the hairs appear to be white. The field notes of collection No. 22770 by C. A. Backer mention the flowers as pale red with brown hairs. Two just opened flowers (Koorders No. 40380, topotypes) were pale brown with whitish caudate appendages. WINCKEL (1918) noted the most divergent colours, viz. the flower as having chestnut brown hairs on an even darker brown wall, while the caudal appendages were flesh coloured at 'anthesis'. This description looks rather like a flower many days old (possibly it never fully opened and hence may have been mistaken for a fresh one).

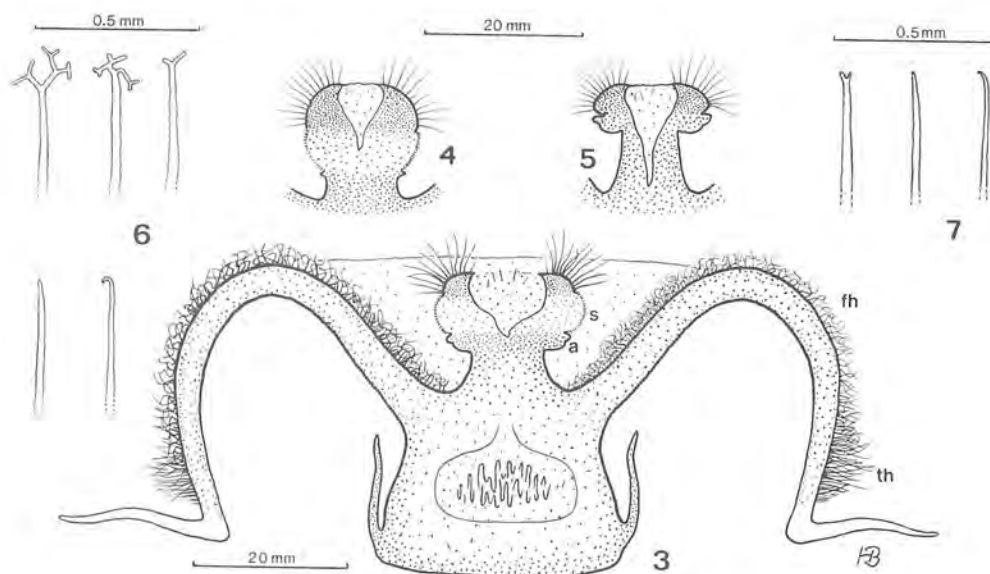
Such discrepant colour description may be due, at least in part, to variations in density of the furry hairs overshadowing or distorting the actual colour of the wall beneath. In addition, following rain, the hair tangle collapses and sticks in a mess to the wall, giving a different appearance. Both effects have been observed by HB in *R. infanticida* but not in *R. deceptor* which lacks furry hairs. Nevertheless, it is possible that *R. zippelii* may be rather variable in colour. Alternatively, it is not excluded that two different taxa may be involved. At any rate, *R. zippelii* is clearly distinguishable from the recognized species on morphological characters, among which most notably the lack of ramenta.

Lack of ramenta has already been stressed by HEINRICHER (1905). None of the more than 20 specimens from Java seen by HB had ramenta. The reason why MEIJER (1997) thought *R. zippelii* had ramenta is probably twofold. He considered *R. deceptor* that he found at Ulu Gadut, which of course has ramenta, to be *R. zippelii*. Secondly, he must have thought that lack of ramenta observed in Javanese taxa was due to secondary factors. He mentions (1997) that the ramenta are often removed by fly activity. However, the ramenta are firmly attached to the base (in an experiment *in vivo*, force was needed to pluck them with forceps), thus flies are incapable of removing them. As showed by BÄNZIGER (1996), not even bees, wasps and most ant species, which all suck nectar from the ramenta pads, cause damage although they have (unlike flies) biting mouthparts; the only exceptions are *Lophomyrmex* ants, which bite off ramenta and nectariferous tissue. But, whenever this occurs, they leave a clearly scarred tepal apex, which remains evident also in preserved specimens. Of all *R. zippelii* studied, only one had scars at the apex, but since no structures remained there, we do not know whether there were any hairs and if so, whether they were ramenta or tuft hairs.

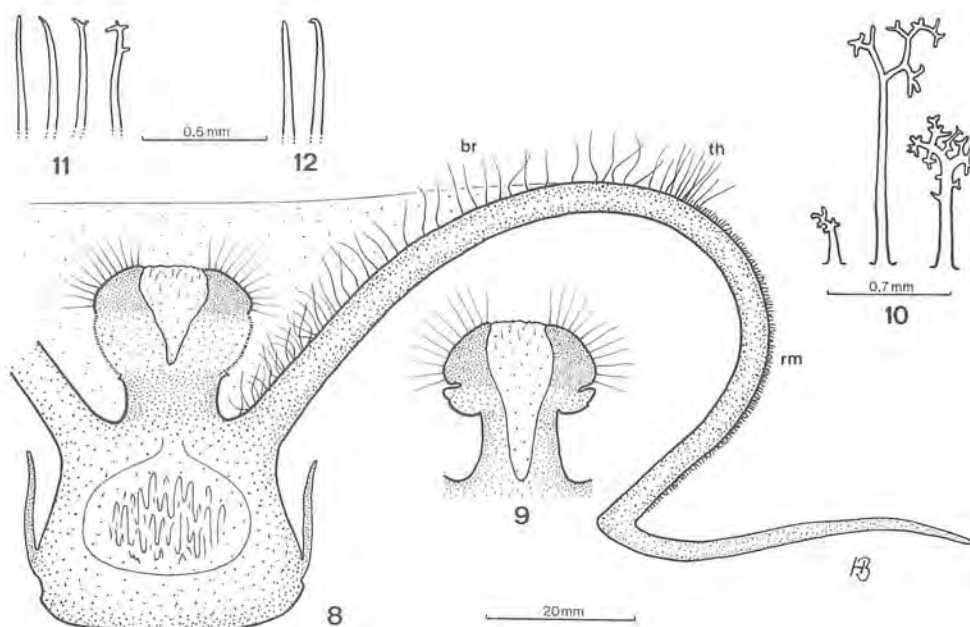
It should also be mentioned that what MEIJER (1997) mentions as ramenta in his Fig. 12g of *R. zippelii*, drawn after Heinricher (1905, Table 3, Figs. 7a–e), are not ramenta but (the endings of) hairs which Heinricher (p 74–75) described as 0.64–0.7 cm long, curved back and forth several times, being of comparable length throughout the tepals, and having unbranched to slightly branched or hooked endings, i.e. furry hairs.

Material studied. INDONESIA, Java. Gunung Salak (SW of Bogor), 24.ii.1922, Daklas, *s. n.*, (bisex. bud); *ibid.* ii.1917, *s.l.*, *s.n.* (No. 16*, bisex. bud); *ibid.* Ciapus Gorge, G. Salak, 500 m, 9. xi.1912, Koorders 40380 (2 bisex. flow., all BO); *ibid.* (*fide* ERNST & SCHMID, 1913, p 5), 1906, A. Ernst, *s.n.* (No. 43, male flow.), UZ; presumably *ibid.* 'Bogor area', *s.d.*, *s.l.* *s.n.*, (No. 17, male flow.), BO. Pasirdatar (SW foothills of Gunung

*For specimens without collector/herbarium number we have used a deliberate code number (set in parenthesis) if the specimen has been morphometrically analysed and mentioned in the appendices.



Figures 3-7. *Rhizanthus zippelii*. Cross-section of bisexual flower (3), of column of female flower (4), of column of male flower (5); enlargements of variously shaped distal part of furry hairs (fh) (6) and tuft hairs (th)(7); a=anther, s=stigmatic fascia.



Figures 8-12. *Rhizanthus lowii*. Cross-section of female flower (8), of male column (9); enlargements of variously shaped ramenta (rm)(10), distal part of bristles (br)(11) and tuft hairs (th)(12).

Pangrango), 2.v.1932, Valetton, *s. n.*, (4 bisex. flow.), all BO. Ibid. 15 or 16.xii.1903, B. v. d. Brink (*vide* HEINRICHER 1905, p 62, Table 1, Fig. 1), (bisex. flow.), UI. Cidadap (S of Cibeber), Gunung Besar, 1000 m, 15.vi.1917, B. v. d. Brink 950, (bisex. flow., bud), BO; *ibid.* Winckel, *s. n.* (No. 7a), (2 bisex. flow., bud); *ibid.* 1100 m, 15.vi.1917, Baker 22770 (2 bisex. flow.); *ibid.* xi.1917, B. v. d. Brink *s. n.*, (1 flow. with anthers but stigma unsure, damaged); *ibid.* but xi.1917, Winckel *s. n.* (No. 11), (2 bisex. flow.); *ibid.* 27.vi.1918, Winckel *s. n.*, (flow., sex undet.). Garut (SE of Bandung), iii.1929, Ader, *s. n.*, (male flow.). Gunung Galunggung (NW of Tasikmalaya), 1930, Ader, *s. n.* (No. 4a, 4c male flow., 4b female bud), all BO.

2. *Rhizanthus lowii* (Beccari) Harms

In Fedde, Rep. 36: 287 (1934); *Brugmansia lowi* [sic] Beccari, Atti Soc. Ital. Sci. Nat. 11: 198 (1868); *Rhizanthus lowi* (Beccari) Harms, emend. Meijer, *Blumea* 33: 337 (1997); Bänziger, Nat. Hist. Bull. Siam Soc. 43: 337 (1995); 44: 113 (1996); *Rhizanthus lowii* [sic] (Beccari) Harms: Meijer, Fl. Males. 13: 39 (1997).

Figs. 8-12, 27-29, 38, Appendix 2.

Description. Bud circumference at anthesis not known but maxima must be well over 250 mm (extrapolation from *R. infanticida*). Flower unisexual. Tepal 90–135 mm long, 10–19 mm wide, caudal appendages 75–85 mm long in males, total span of flower (incl. caud. app.) 250–430 mm. Basal 1/3–2/3 of tepal length covered by bristles which sparsely set (35–67 per cm² near tepal vertex, denser opposite globular head, 200–250 per cm², where more curved and overlapping), comparatively stiff (0.045–0.07 mm in diameter and 0.002–0.006 mm wall thickness), 9–11 mm long, mostly with un- or only shortly bifurcated tips. Tuft hairs 7–10 mm long, 0.06–0.07 mm in diameter and 0.004–0.006 mm wall thickness, with relatively low density of 450–800 per cm². Distal 1/3–2/3 of tepal length covered by strongly branched (up to nearly 30 endings) ramenta 0.3–1.2 mm long, 0.03–0.1 mm in diameter, on a 26–89 mm long, 5–16 mm broad pad.

Column 21 mm high in females, 13–17 mm in males; style 5.5 mm high and 11–15 mm wide in females, 5–7 mm high and 9–13 mm wide in males; globular head 15.5 mm high in females, 9–10.5 mm in males. Ampulla wall 9 mm long in females, 7–7.5 mm in males; ampulla diameter 20–25 mm in females, 17.5–22 mm in males; its crater aperture 12 mm in females, 9–12 mm in males; crater depth 17 mm in females, 19–21 mm in males. Stigmatic fascia 9 mm wide, annular row of anthers 4–6 mm, number of anthers 50–70. Narrowest female neck 42 mm wide, broadest 57 mm, narrowest male neck 23–30 mm.

Colour. Tepal base pale with brownish radial lines, more distally becoming gradually darker, brownish to reddish brown, with or without yellowish or whitish speckles, blotches or marbling, the area with ramenta brown to dark brown, the caudal appendages reddish brown or fleshy, sometimes with paler bases; column pale yellowish, ampulla reddish brown to brownish, bristles cinnamon to brown, ramenta brown.

Diagnosis. See key. Additional differences: tuft hairs are least dense (450–800 hairs per cm², 500–2500 in the other spp.) and not so evident. The anthers are the most numerous (50–70, in other spp. 31–54), and the tepals and caudal appendages are the longest, lending the flower the largest total span of 250–430 mm, up to twice that of the smallest species, *R. infanticida*.

Biology. Habitat: tropical rain forests at low elevations, up to 350 m. Darnaedi's D.2652 from 1400 'm' may have referred to feet, hence only 470 m. Host: in the area of Kuala Belalong, Batu Apoi Forest Reserve, Brunei, 120–160 m asl, all 7 clusters studied by HB infected exclusively *T. pedunculare*; *T. papillosum* was not seen in the neighbourhood. Identification of the lianas is based on the description mentioned in BÄNZIGER (1995) and on material (complete with fruits) at BFC identified by A. Latiff.

Distribution. Borneo.

Material studied. INDONESIA, Borneo. E Kalimantan, Gunung Tapian Lobang, on Menubar River, 100 m, (40–50 km NNE of) Sankulirang (about 190 km NE of Samarinda), s. d., Kostermans 6156a (male bud), 6156b (female flow.). Loa Haur, W of Samarinda, 40 m, 16.v.1952, Kostermans 6971 (3 buds, dry coll.). Kalimantan, Sungai Raoen, 7–14.iv.1894, Hallier 3091 (2 male buds, 1 bud closed). S. Pamilan, Gunung Seribu, 1400 (probably feet), 6.viii.81, Darnaedi D.2652 (2 male buds), all BO.

BRUNEI (Borneo). Kuala Belalong, 100 m, 6.v.1992, 920506–1/8B, (male flow., 3 buds). Ibid., Batu Apoi Forest Reserve, 120–160 m, x. 1998, Patiño s. n., (opening male flow.), all at BFC.

EAST MALAYSIA (Borneo). Sabah, Tenom Distr., Melalap Valley, 250–350 m, 4.xi.1997, Kocyan AK 971104/1/01 (1 freshly opened male, 1 female column and ovary of otherwise mutilated old flower), coll. A. Kocyan.

3. *Rhizanthès infantìcida* Bänzìger et Hansen sp. n.

Rhizanthès lowii auct. non (Beccari) Harms: Molesworth Allen, Mal. Nat. J. 21: 29 (1968). Meijer, Flora Malesiana I, 13: 40 (1997).

Rhizanthès zippelii auct. non (Blume) Spach: Meijer & Veldkamp, Blumea 33: 339 (1988). Bänzìger, Nat. Hist. Bull. Siam Soc. 43: 337 (1995); 44: 113 (1996); 45: 156 (1997).

Figs. 13–17, 22–24, 30; Appendices 3–4.

A specie Rhizanthès zippelii pariete tepali basim versus subflavi, non eburnei, apicem versus spadiceis ad roseum canum, non pallidae carnis coloris; ramentis praesentibus 1/20 ad 1/5 apicem versus longitudinis tepali, non absentibus; caudalis additamentis spadiceis ad subroseum, non albidis coloris; unisexuali, non unisexuali aut bisexuali differt. A specie Rhizanthès lowii floribus minoribus, 143–220 mm, non 250–430 mm spatio; maiore parte tepali nexu denso mollis pilis, non duris setis sparsis oblecta; ramentis 1/20 ad 1/5 apicem versus tepali, non 1/3 ad 2/3, praesentibus differt. A specie Rhizanthès deceptore pariete tepali basim versus subflavi et apicem versus spadiceis ad roseum canum, non albi coloris; maiore parte tepali nexu denso mollis pilis, non duris setis sparsis oblecta differt.

Etymology. From Latin, *infanticida* means to kill young children. The epithet alludes to the flower's pollination syndrome leading to the death of the pollinators' brood.

Description. Bud circumference at anthesis 147–205 mm (average 170 mm). Flower unisexual. Tepal 58–90 mm long, 9–20 mm wide, caudal appendages 20–38 mm long in females and 25–51 mm in males, total span of flower (incl. caud. app.) 143–220 mm. Except distally, tepal covered by furry hairs which densely set (600–1400 per cm² near tepal vertex, generally less dense opposite ampulla, 400–800 hairs per cm², where of slightly larger diameter, thicker walls), 6–8 mm (sometimes up to 11 mm) long, pliable (0.025–0.05 mm in diameter 0.0018–0.0035 mm in wall thickness), with hooked, bifid, or

sometimes un- to multi-branched endings. Distally to the furry hairs tuft hairs, even more densely set (500 to more than 2000 hairs per cm²), 7.5–11 mm long, 0.04–0.06 mm in diameter and 0.004–0.007 mm wall thickness. Distal 1/20–1/5 of tepal length covered by non- to multi-branched (up to 8 endings) ramenta 0.5–2 mm long, 0.03–0.065 mm in diameter, on a nectariferous pad 3–14 mm long and 2–11 mm broad.

Column 18–22 mm high in females, 12.5–16 mm in males; style 4.5–6 mm high and 8–12 mm wide in females, 5–7 mm high and 7–8 mm wide in males; globular head 13–16 mm high in females, 7–10 mm in males. Ampulla wall 6.5–8.5 mm long in females, 4–7 mm in males; ampulla diameter 16–20 mm in females, 13–17 mm in males; its crater aperture 8.5–11 mm in females, 7–11 mm males; crater depth 8–10 mm in females, 11–17 mm in males, ampulla hairs 3–6 mm long outside, shorter or lacking inside. Width of stigmatic fascia 6.5–9.5 mm, annular row of anthers 3–4 mm, number of anthers 31–52. Narrowest female neck 28–42 mm wide, broadest 31–44 mm, narrowest male neck 20–29 mm.

Colour. Tepal base pale yellowish with brownish radial lines, more distally tepal yellowish to pale brownish to greyish with faint pinkish tinge, pad with ramenta dark brown, caudal appendages and ampulla reddish brown or fleshy, column pale yellowish, furry hairs cinnamon, tuft hairs and ramenta dark brown.

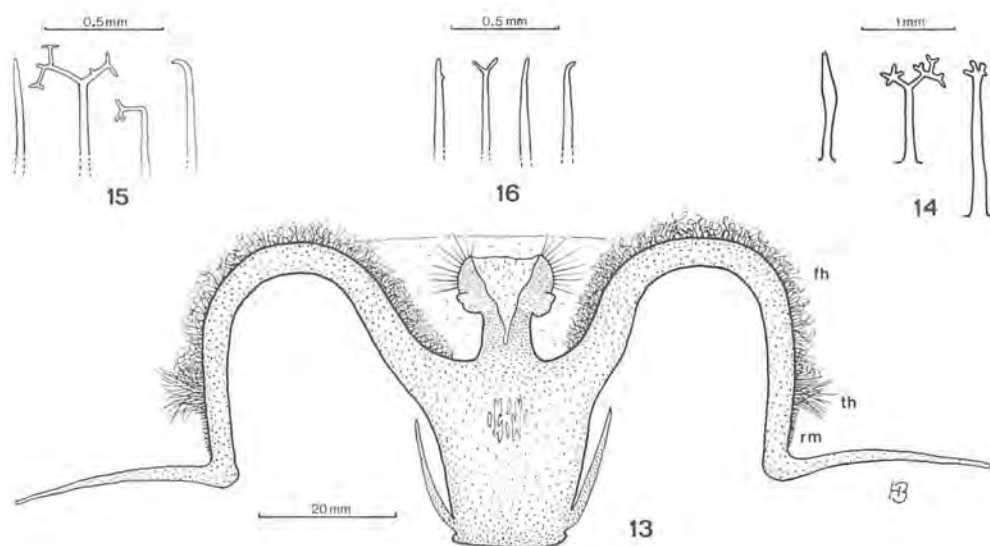
Distribution. S Thailand (Narathiwat-type), W Malaysia and Sumatra.

Diagnosis. See key. Additional differences: female *R. infanticida* tend to have the largest crater aperture (ratio crater aperture:ampulla diameter 0.5–0.7, in *deceptor* 0.3–0.4, in *lowii* and unisexual *zippelii* 0.5), the highest globular head (ratio height globular head:ampulla diameter 0.7–0.9, in *deceptor* 0.5–0.6, in *lowii* 0.6–0.7, in *zippelii* 0.6), the widest stigmatic fascia (ratio stigmatic fascia:ampulla diameter 0.4–0.5 against 0.3–0.4 in the other species), and the least curved, most vertically set ampulla walls. Contrary to the other 3 spp., the hair density opposite the ampulla is generally lower than near the vertex of the reflexed tepal.

Biology. Habitat: tropical rain forests, in Thailand and Malaysia only lowland, up to 450 m, in Sumatra at mid elevations, 950–1050 m. Host: all 27 clusters studied in S Thailand and W Malaysia infected exclusively *T. pedunculare*, 8 clusters in W Sumatra infected exclusively *T. papillosum* (BÄNZIGER, 1995 and in prep.; identifications based on flowering and fruiting specimens). Morphological and ecological notes on the lianas, details on anthers, stigma, pollen, nectar, odours, bud growth, anthecology and population structure of *R. infanticida* in *loc. cit.* As a sapromyophilous flower, pollination is based mainly on brood-site deception with nectar as a minor reward, carried out by females of up to 10 species of carrion flies (Calliphoridae). *R. infanticida* is so devastatingly effective in dissimulating a mammalian carcass as to mislead the pollinator into laying hundreds of eggs the hatchlings of which will die of starvation. Hence the pollination system is different from that of *Rafflesia* and *Sapria* (BÄNZIGER, 1996 and in prep.).

Remarks. W Sumatran individuals tend to have smaller ramenta pads, viz. 3–6 mm long, less branching of ramenta, while the flowers are in the upper size range.

Vernacular name. It appears there is no Thai name. The restricted area in extreme S Thailand where *R. infanticida* was discovered as recently as 1995, is inhabited by Malay speaking people. As mentioned in BÄNZIGER (1995), it is not clear whether the name ดอกบัวครึ่ง (dok bua khrang, lacquered lotus flower) listed in Smitinand (1980) actually refers to this plant and is not, like ดอกบัวผุด and ดอกบัวตูม (dok bua phud, dok bua tuum,



Figures 13-16. *Rhizanthus infanticida*. Cross-section of male flower (13), enlargements of variously shaped ramenta (rm)(14), distal part of furry hairs (fh)(15) and tuft hairs (th)(16).

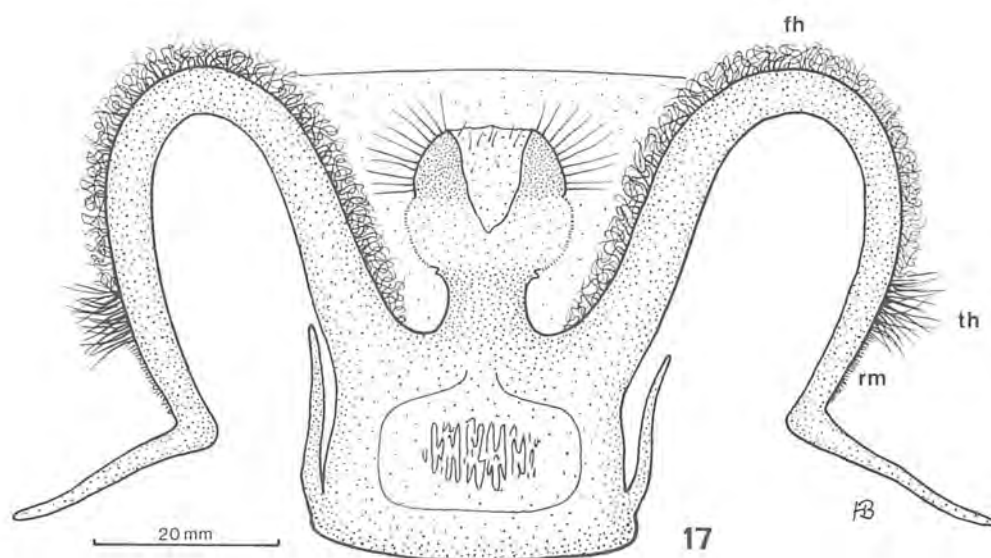


Figure 17. *Rhizanthus infanticida*. Cross-section of female flower. rm=ramenta, fh=furry hairs, th=tuft hairs.

sprouting lotus), one of several names applied to *Rafflesia kerrii*. As a possible name we suggest ดอกแมงกะพรุน (dok maeng kaphrun, medusa flower), the many tepals with caudate appendages appearing like the tentacles of a medusa, the campanulate tube its bell (campanula and bell actually are cognate), and the ampulla's crater aperture its mouth (though it is in ventral position in medusae). Medusa flower is a more poetic name than mammalian carcass flower, the model *R. infantcida* mimicks.

Material studied. Holotype. Female, THAILAND, Narathiwat Prov., Phu Khao Thong, 375 m, 1.iv.1996, Bänziger 1546, BKF. Paratypes. Ibid. but 270–375 m, 31.iii., 13–18.iv.1995, 1–9.iv.1996, 10.ii.2000, Bänziger 1538–1545, 1547–1549, 1722 (4 females (1 bud), 8 males (1 bud)), to be deposited at BKF, except 1542, 1548 to Copenhagen (C).

Non-type material. MALAYSIA, Perak State, E of Chenderiang, 330–450 m, 24–25.i., 1–3.ii.1994, 17–31.i.1995, Bänziger 1516–1537 (6 females (5 buds), 16 males (3 buds)), to be deposited at Herbarium University Kebangsaan (Bangi, Malaysia), except 1518, 1530 to BKF, 1522 to AU, 1525, 1534 to UZ and 1531, 1533 to UI (material originally used for studies of Bänziger 1995, 1996, none collected since). INDONESIA, only two live specimens (buds) collected: W Sumatra, Batang Palupuh, about 1000 m, 16.vii.1998, 22.viii.1999, Bänziger 1713, 1714, to AU and BKF. Dead, incomplete specimens: ibid. but 12–13.vii.1998, Bänziger 1705–1710 (dead parts of 3 females, 3 males), to AU and BKF. Four freshly opened male flowers not collected, only photographed and measured in the field.

4. *Rhizanthus deceptor* Bänziger et Hansen sp. n.

Rhizanthus zippelii auct. non (Blume) Spach: *partim* Meijer & Veldkamp, Blumea 33: 338, 340 (1988); *partim* Meijer, Flora Malesiana I, 13: 40 (1997).

Figs. 18–21, 25, 26, 31–33; Appendix 5.

A specie Rhizanthus zippelii maxima parte parietis tepali duris setis sparsis, non nexu denso mollis pilis oblecta; ramentis praesentibus 1/15 ad 1/5 apicem versus longitudinis tepali, non absentibus; tepalum album (pulvino fuscis ramentis excepto), non 1/2 ad 2/3 basim versus eburneis neque 1/3 ad 1/2 apicem versus pallidae carnis coloris; caudalis additamentis ad subroseum spadiceis, non albidis; unisexuali, non unisexuali aut bisexuali differt. A specie Rhizanthus lowii maxima parte tepali albis, non subflavis aut spadiceis; ramentis 1/15 ad 1/5 apicem versus tepali, non 1/3 ad 2/3, praesentibus; ramentis, non cum ramis vel quam maxime modicis ramis, non cum multis ramis differt. A specie Rhizanthus infantcida maxima parte parietis tepali duris setis sparsis, non nexu denso mollis pilis oblecta; tepalum album (pulvino fuscis ramentis excepto), non basim versus subflavum et apicem versus spadix ad roseum canum differt.

Etymology. From Latin, alludes to *Rhizanthus*'s notoriety in deceiving flies and scientists alike.

Description. Bud circumference at anthesis 200–225 mm (only 3 measurements so far available). Flower unisexual. Female (no males found): tepal 75–100 mm long, 10–27 mm wide, caudal appendages 27–32 mm long, total span of flower (incl. caud. app., extrapolated for males) 203–270 mm. Except distally, tepal covered by bristles which sparsely set (20–30 per cm² near tepal vertex, 150–200 per cm² opposite the globular head, where more sinuous), comparatively stiff (0.06–0.09 mm in diameter and 0.004–0.007 mm wall thickness), 7–10 mm long (exceptionally more than 13 mm), often non-branched but when

branched only little so and at the very tip only. Distally to the bristles a patch of 3–6 x 5–10 mm bearing tuft hairs which densely set (500–1500 hairs per cm²), 8–12 mm long, 0.09–0.1 mm in diameter and 0.006–0.01 mm in wall thickness, with pointed tips, rarely slightly hooked or a simple tiny branching. Distal 1/15–1/5 of tepal length covered by non-to moderately-branched ramenta (but sometimes with up to 8 endings), 0.8–2 mm long, 0.05 mm in diameter, on a 5–11 x 7–17 mm nectariferous pad.

Height of column 19–23.5 mm, of globular head 13–17 mm, of style 6–9 mm, its width 8–13 mm. Ampulla wall 9.5–11.5 mm long, ampulla diameter 17–27 mm, its crater aperture 6–10 mm, crater depth 8–11 mm, its hairs on the outside 4–9 mm long, inside 3–5 mm long. Width of stigmatic fascia 6–7 mm, number of radial lines (= number of anthers, rudimentary in females) 46–54. Narrowest female neck 31–42 wide, broadest 33–51 mm.

Colour. Tepal white throughout except, basally, the brown radial lines and, distally, a dark brownish area bearing tuft hairs and ramenta; a small greyish area proximal to the latter may be present; caudal appendages reddish brown, column pale yellowish, ampulla reddish brown but with a more brownish tinge than in *R. infantida*, bristles cinnamon to brown, tuft hairs and ramenta brown to dark brown. The part of the tube opposite the column appears brownish but this is deceptive: it is an overshadowing effect by the more densely set bristles and the convergence of the radial lines, the wall there being as white as elsewhere.

Distribution. Sumatra (West Sumatra-type).

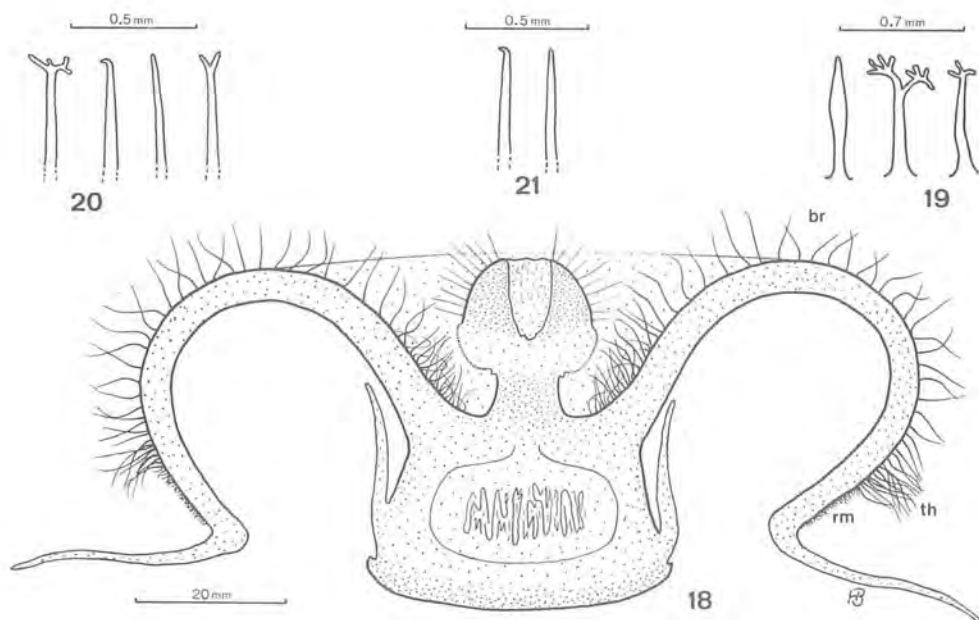
Diagnosis. See key. Additional differences: female *deceptor* tend to have the most conically-shaped ampulla, the smallest crater aperture (ratio crater aperture:ampulla diameter 0.3–0.4, in *infantida* 0.5–0.7, in *lowii* and unisexual *zippelii* 0.5) and, when compared with the length of the ampulla wall, the narrowest stigmatic fascia (ratio 0.5–0.7, in *lowii* 1.0, in *infantida* 0.9–1.4, in unisexual *zippelii* 0.9).

Biology. Habitat: tropical rain forest at mid elevations, 500–700 m. Host: 3 clusters on the left side of a stream infected *T. pedunculare* (e.g. Bänziger No. 1692, 1693), 5 clusters on the right infected *T. papillosum*. Pollinators included carrion flies *Chrysomya defixa* (Walker), *Lucilia porphyria* (Walker), *Hypopygiopsis fumipennis* (Walker) (Bänziger, in prep.).

Remarks. Unfortunately no male was found. The white colour persisted unchanged during the first 3 days of anthesis. MEIJER and VELDKAMP (1988) and MEIJER (1997) considered this species as *R. zippelii* probably on the ground of its white colour, but the morphological differences with it are clear and not less marked than with *R. lowii*.

Material studied. Holotype. Female, INDONESIA, W Sumatra, Ulu Gadut, E of Padang, 645 m, 5.ix.1999, Bänziger 1721, to AU. Paratypes. Ibid. but 24–31.viii., 2.ix.1999, Bänziger 1716–1720 (all females, 2 flowers, 3 buds, one of which collected dead), to AU, BKF, C.

Non-type material: INDONESIA, W Sumatra, Ulu Gadut, E of Padang, about 500 m, 21.vi.1990, W. Meijer, s. n., (4 buds). Bengkulu, s. d., Sugeng Reksodiharjo, s. n., (bud), all in BO.



Figures 18-21. *Rhizanthus deceptor*. Cross-section of female flower (18), enlargements of variously shaped rammenta (rm)(19), distal part of bristles (br)(20) and tuft hairs (th)(21).

INCOMPLETELY KNOWN TAXA AND PROBLEMATIC SPECIMENS

Specimens collected by de Wilde & de Wilde-Duyfjes 12148, L, and Assist. Res. A. Dirks 1000/184 and Lorzing 5434, both BO, all from Sumatra, have the basal half of the flower white, set in abrupt contrast to the dark distal half. The rammenta are probably like those of *R. lowii*. Since we have not seen fresh specimens for a careful analysis, we have to desist from formal taxonomic treatment of this entity.

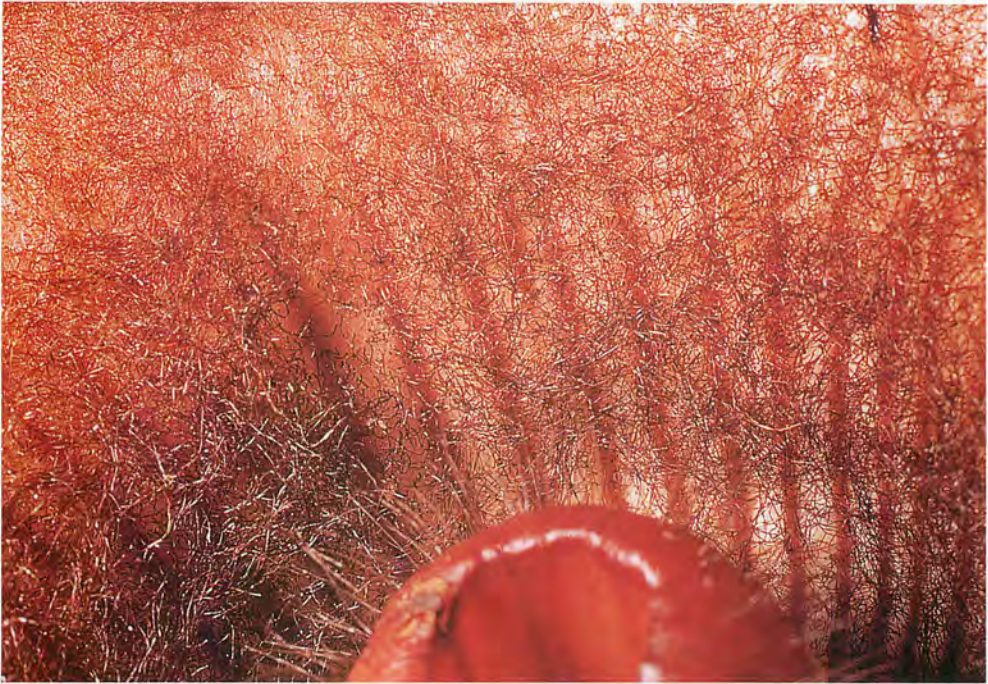
Specimens collected by H. O. Mayr 161, Groeneveldt *s. n.* (vii.1918), and Japing *s. n.* (iv.1930), from Sumatra, all BO, seem to lack rammenta. Again, the preserved material does not allow clear evaluation of other characters. The specimens may be extreme cases of *R. infanticida*, which in Sumatra tend to have smaller rammenta patches than in the Malay Peninsula, but it cannot be excluded that they may represent *R. zippelii*, otherwise known only from Java.



22



23



24

Figures 22–24. *Rhizanthes infantica*. Male flower; note radial lines (22); distal part of tepal with upstanding tuft hairs, patch of ramenta (with a *Meranoplus* ant imbibing nectar), and caudal appendage (23); detail of tepal area between vertex and ampulla showing dense tangle of furry hairs (24).



Figure 25. Female *Rhizanthese deceptor*, about 12 hours after the flower started to open around midnight.



Figure 26. Detail of *Rhizanthese deceptor* showing tepal with sparsely set bristles. The fly is *Chrysomya defixa*, nearly 1 cm long.



Figure 27. Male *Rhizanthus lowii*. Note the very long ramenta pad. (Photo A. Kocyan).



Figure 28. Detail of *Rhizanthus lowii* showing tepal area opposite the ampulla with relatively sparsely set bristles. The fly is probably *Chrysomya defixa*, about 1 cm long. (Photo A. Kocyan).



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31



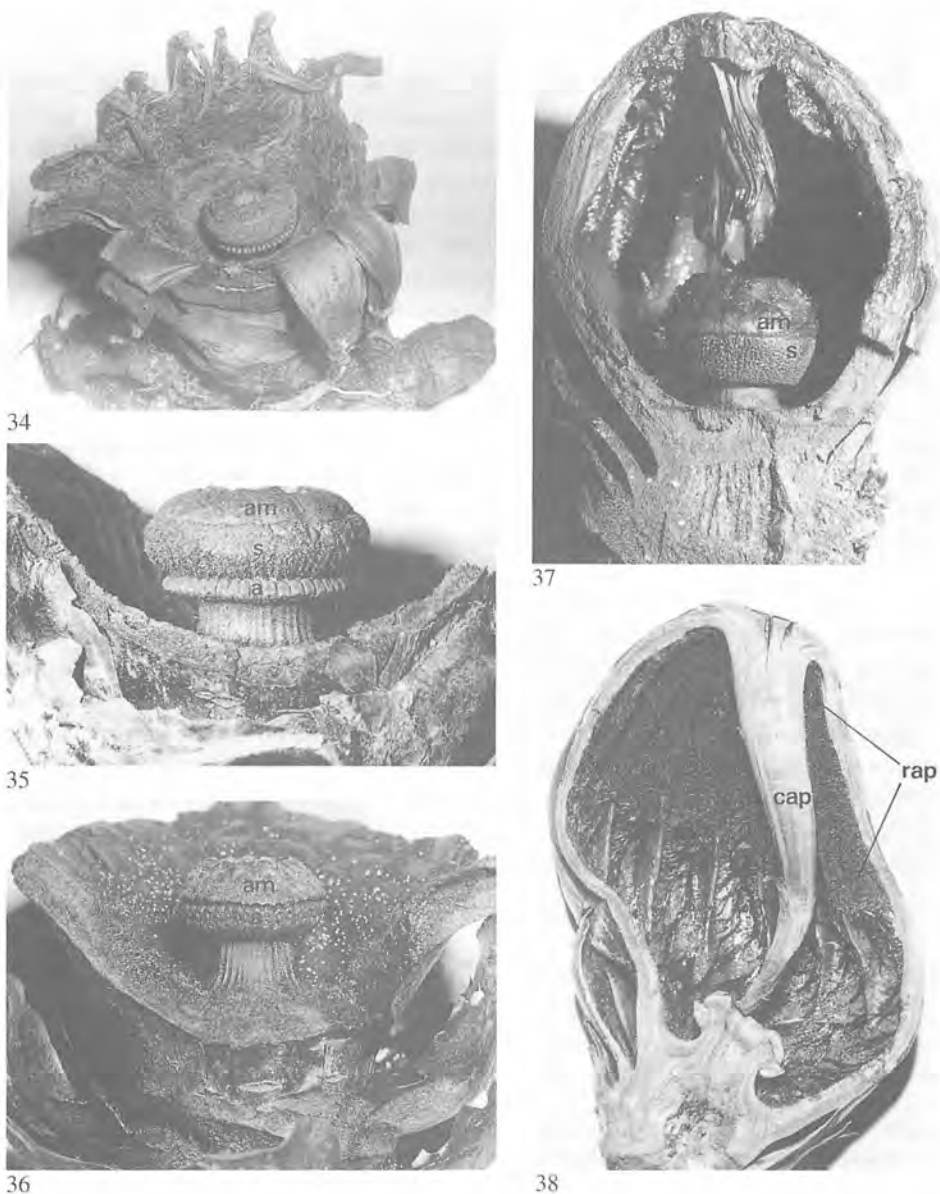
32



33

Figures 29–31. Cross-sections of *Rhizanthus* buds. Mature *R. lowii* male, note very long ramenta pads taking up 2/5 of distal tepal (29) (Photo A. Kocyan); male *R. infanticida*, large (circumference 13.6 cm), note dense tangle of furry hairs (30); female *R. deceptor*, large (circumference 17.7 cm), note relatively sparse, thick bristles on pale tepal wall (31).

Figures 32–33. *Rhizanthus deceptor*. Three days old flower (32); detail of tepal showing bristles, tuft hairs and ramenta (33).



Figures 34–37. Ethanol-preserved *Rhizanthes zippelii*. Bisexual flower. Pasirdatar, 1903 (34). Bisexual flower, frontal view, Gunung Besar, 1917 (35). Male flower, Gunung Salak, 1906 (36). Cut-open mature female bud (circumference 151 mm), Gunung Galunggung, 1930 (37). a=anthers, s=stigmatic fascia, am=ampulla.

Figure 38. Cut-open, ethanol-preserved, mature male bud of *Rhizanthes lowii* (circumference 250 mm). Note the very long pad with ramenta. Gunung Tapian Lobang, E Kalimantan. rap=ramenta pad, cap=caudal appendage.

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REFERENCES

- BÄNZIGER, H. 1995. Ecological, morphological and taxonomic studies on Thailand's fifth species of Rafflesiaceae: *Rhizanthus zippelii* (Blume) Spach. *Nat. Hist. Bull. Siam Soc.* 43: 337–365.
- BÄNZIGER, H. 1996. Pollination of a flowering oddity: *Rhizanthus zippelii* (Blume) Spach (Rafflesiaceae). *Nat. Hist. Bull. Siam Soc.* 44: 113–142.
- BÄNZIGER, H. AND B. HANSEN. 1997. Unmasking the real identity of *Sapria poilanei* Gagnep. emend., and description of *Sapria ram* sp. n. (Rafflesiaceae). *Nat. Hist. Bull. Siam Soc.* 45: 149–170.
- HEINRICHER E. 1905. Beiträge zur Kenntnis der Rafflesiaceae. I. *Denkschr. K. Akad. Wiss. Wien, mathem.-naturw. Kl.* 78: 57–81.
- MEIJER, W. 1997. Rafflesiaceae. *Flora Malesiana* I, Vol. 13: 1–42.
- MEIJER, W. AND J. F. VELDKAMP. 1988. A revision of *Rhizanthus* (Rafflesiaceae). *Blumea* 33: 329–342.
- MEIJER, W. AND S. ELLIOTT. 1991. Taxonomy, ecology and conservation of *Rafflesia kerrii* Meijer in southern Thailand. *Nat. Hist. Bull. Siam Soc.* 38: 117–133.
- SMITINAND, T. 1980. *Thai plant names*. Funny Publishing, Bangkok.
- WINCKEL, W. F. 1918. *Brugmansia zippelii* Bl. *De Tropische Natuur* 7: 81–88.

Appendix 1. Morphometric data of *Rhizanthes zippelii* (in mm; ethanol preserved).

Flower or bud Sex Code No.	Flower bisexual (7a)	Flower bisexual 950a	Flower bisexual (11)	Flower bisexual 40380a	Bud* bisexual 40380b	Bud bisexual 950b	Bud bisexual (16)	Bud female (4b)	Flower male (4a)	Flower male (4c)	Flower male (17)	Flower male (43)
Width of flower (without caudal appendages)	**	**	130	124	—	—	—	—	190	160	126	**
Length of caudal appendage	**	**	—	20	15–20	20	14–16	20	47–50	57	16	**
Length/ width of tepal	**	**	60–65/ 8–10	65–70/ 14	50/ 10–13	70/ 9–15	55/ 10–12	70/ 8–12	100/ 1—	90/ 10–17	60/ 16	**
Height of column	16	17	14	16	19	14.5	14	16	17	18	13	14
Height/width of style	5/ 12	5/ 11.5	—/ 1—	5/ 1—	—/ 1—	4.5/ 11.5	2.5/ 13.5	3/ 10	7/ 10	9/ 1—	5/ 8	6.5/ 8
Height of globular head	11	12	—	11	12	10	11.5	13	10	9	8	7–8
Height of ampulla/ length of ampulla wall	3.5/ 5	3.5/ 1—	—/ 1—	3.5/ 6	—/ 1—	4/ 1—	3.5/ 6.5–7	7.5/ 9	6/ 6.5	—/ 7	4/ 5	4–4.5/ 5–5.5
Diameter of ampulla	23	23	16	20	18–21	21.5	23	19–24	17–18	17	15	15.5
Crater aperture	10–11	11	—	9.5–10	12–14	8	9	9–12	9–11	8–10	9	9
Crater depth	7	6.5	7	7	8	7	7	7	17	18	12	17
Width of stigmatic fascia/annular row of anthers	5.5/ 12	6.5/ 13.5	—/ 1—	4/ 1—	—/ 1—	5/ 13.5	6/ 14	6.5/ 1—	—/ 14	—/ 1—	—/ 14	—/ 14
Number of anthers	47	48	46	44	—	—	—	—	54	50	45	42

Code Nos. in parenthesis are provisional for BO or UZ collections s.n. *This bud is already opening. **Damaged.

Appendix 2. Morphometric data of *Rhizanthus lowii* (in mm; ethanol preserved)

Flower or bud Sex Code No.	Flower female 6156b	Flower female (AKa)	Flower male (AKb)	Bud male D.2652a	Bud male 6156a	Bud male 3091a	Bud male 3091b
Width of flower (without caudal appendages)	260	damaged	210	—	—	—	—
Length of caudal appendage	>32	damaged	60	>55	85	85	75
Circumference of bud	—	—	—	175	250	207	208
Length/width of tepal	135/19	damaged	95–105/15–20	70–80/9–14	100/12–18	120/11–15	90–95/10–17
Length/width of ramenta pad	45/15	damaged	28–33/11–16	26–29/5–10	38–48/10–15	89/15	41–52/10–15
Height of column	21	23	14	16	13	17	17
Height/width of style	5.5/15	7.5/11	6/9	5.5/10	4/13.5	7/12	7/11
Height of globular head	15.5	15	8.5	10.5	9	10	10
Height of ampulla/ /length of ampulla wall	6/ /9	6.5/ /9	6/ /7	6/ /7	5.5/ /7	6/ /7.5	6.5/ /7
Diameter of ampulla	25	20	17.5	17.5	22	19–21	20
Crater aperture	12	9	8.5	—	11	9–12	9–10
Crater depth	17	13	15.5	—	19	20	21
Width of stigmatic fascia /annular row of anthers	9/ /—	8.5/ /—	—/ /4–5	—/ /4–5	—/ /4–5	—/ /4–5	—/ /4–6
Number of anthers/ /(radial lines in female)	—/ /—	—/ /60	64/ /—	63/ /—	70/ /—	67/ /—	69/ /—
Narrowest/widest width of neck	42/57	33/45	25/—	23/—	—/—	30/—	27/—

(AKa) and (AKb) stand for AK971104/01 female and male flower, respectively.

Appendix 3. Morphometric data of female *Rhizanthès infanticida* (in mm; ethanol preserved)

Flower or bud Present code No. Previous (1995) code No.	Flower 1538 5W	Flower 1539 9.1	Flower 1546 —	Flower 1518 0.3	Flower 1722 —	Bud 1525 1.2
Width of flower (without caudal appendages)	175–180	120	150	140–145	135–140	—
Length of caudal appendage	20–33	23–29	25–38	28	30–40	27–31
Circumference of bud	—	—	—	—	—	171
Length/width of tepal	90/11–20	65/10–15	—/14–20	80/13–16	70/12–17	58/9–13
Length/width of ramenta pad	10/6–8	4–6/4–6	9/—	6–8/5–7.5	5–7/4–5	6–8/4–6
Height of column	21–22	20	19	20	19.5	18–19
Height/width of style	5.5/12	5/8	4.5/9.5	6/9	5.5/8	5.5–6/9
Height of globular head	16	15	14.5	14	13.5	13
Height of ampulla/ length of ampulla wall	6.5–7.5/ /7	7–7.5/ /7.5–8	6–7/ /7–8	7/ /7.5–8.5	7.5/ /8	6–7/ /6.5–7
Diameter of ampulla	19	16	17	18–20	15	17.5
Crater aperture	11	10	11	10–11	7	8.5–9.5
Crater depth	10	9	9.5	10	11	8
Width of stigmatic fascia	9.5	7.5	8	7	7	6.5–7
Number of radial lines	*	*	*	*	48	*
Narrowest/widest width of neck	42/44	32/35	—/34	33/35	28/31	33/35

*Not counted.

Appendix 4. Morphometric data of male flower of *Rhizanthus infantidica* (in mm; ethanol preserved).

Present code No. Previous (1995) code No.	1541 5.Z	1542 5.1	1543 5.2	1547 —	1519 0.4	1522 0.7	1530 2.4	1531 2.5.1
Width of flower (without caudal appendages)	165	145–150	150–157	150	165–175	140–145	155–160	137–147
Length of caudal appendage	30–40	30–40	30–40	27–50	35–45	25–35	38–51	30–35
Length/ /width of tepal	80–83/ /11–20	70–75/ /13–16	70–75/ /13–19	75/ /6–14	75–80/ /12–19	65–67/ /10–17	75–80/ /13–19	62–65/ /12–15
Length/ /width of ramenta pad	10–12/ /5–8	8–9/ /5–8	10/ /5–9	9–11/ /5–9	8–12/ /6–9	8–12/ /5–8	11–14/ /5–11	10–11/ /5–7
Height of column	16	13	14	13–14	15.5	13	14	12.5
Height/width of style	6/8	5/8	6/8	6–7/8	6.5/8	5/7	6/7	5.5/8
Height of globular head	10	8	8	7	9	8	8	7
Height of ampulla/ /length of ampulla wall	6/ /6	5/ /5	5/ /5	3.5–4/ /4–5	6/ /7	5/ /5	5.5/ /6	4.3/ /5
Diameter of ampulla	17	16	15–17	13	15	13–14	14	16
Crater aperture	9–10	9–10	8–11	7–8.5	8	7–8.5	9	8–9
Crater depth	15	15	15	17	15	12	12	11
Width of annular row of anthers	4	3	3	3.5	3.5	3	4	3
Number of anthers	48	51	50	41	41	46	40	48
Narrowest width of neck	29	25	28	24	—	20	23	24

Appendix 5. Morphometric data of female *Rhizanthès deceptor* (in mm; ethanol preserved, except where field measurements).

Flower or bud Code No.	Flower 1720	Flower 1719	Flower 1721	Flower *	Flower *	Bud 1717
Width of flower (without caudal appendages)	200	175	180	175	140	—
Length of caudal appendage	27	28–32	30	damaged	damaged	30
Circumference of bud at anthesis ¹	225	200	210	—	—	(175) ²
Length/width of tepal	90–100/15–27	85/15–19	90–95/16–18	80/12–17	75/10–15	75/11
Length/width of ramenta pad	11–13/6–11	9.5–11/6–8	7–12/5–8	17/8	10/8	9/5
Height of column	23.5	21	21	23	19	18
Height/width of style	6–6.5/8	6/8	6/8.5	9/11–13	6/12	5.5/9
Height of globular head	17	14.5	15	14	13	13
Height of ampulla/ length of ampulla wall	9.5/ /11.5	9/ /10.5	8/ /9.5–10.5	7/ /10	6/ /10	7/ /9
Diameter of ampulla	20	17	17	24–27	23–25	19.5
Crater aperture	7.5–8.5	6–7	6–6.5	7–10	6–9	7
Crater depth	10.5	11	10	8.5	8	12
Width of stigmatic fascia	7	6	6.5	7	7	6.5
Number of radial lines	54	47	46	**	**	—
Narrowest/widest width of neck	34/38	31/33	31/36	42/51	over 40	35/40

*Not collected, field measurement. **No more evident. ¹Extrapolation of field measurements effected about 6 h before opening started, except ² which not yet mature.

