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RAFFLESIACEAE

(W. Meijer, Lexington, U.S.A.)[1]

Rafflesiaceae Dumort., Anal. Fam. Pl. (1829) 14; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 1–128; Meijer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 557–563; Hansen in Fl. Thailand 2 (1972) 182–184; in Fl. Camb., Laos & Vietnam 14 (1973) 59–64; Kiu & Wing in Fl. Reipubl. Pop. Sin. 24 (1988) 246–248; Dell in Fl. Austral. 22 (1984) 147–150.

Parasitic plants, rootless, without chlorophyll, always rich in tannins, monoecious or dioecious. *Endophytic body* as strings (chains) or plates of cells inside host plant. Flowering buds or flowering branches vascularized, bursting through the cortex of the host and terminating in a single flower or in short racemes or spikes, with series of scales (bracts) at the base of the buds. *Flowers* uni- or bisexual; perianth single (perigone), often tubular or saucer-shaped at base, in *Rafflesia* and *Sapria* the apex of the tube partly closed by a diaphragm; stamens grouped around a central column representing part of the pistil in female and bisexual flowers, often joined with that column; ovary unilocular, in general inferior but in some cases semi-inferior or superior (*Mitrastema*), with 4–6 or numerous parietal placentas. *Fruits* berry-like. *Seeds* minute, surrounded by pulp, testa hard, often thickened and pitted, embryo few-celled, undifferentiated.

DISTRIBUTION

As defined here the family is subdivided into two subfamilies with a total of nine genera and about 40 species, mainly in tropical regions, although some species occur in subtropical and even temperate parts of the world. The three genera of the tribe *Rafflesieae* of the subfamily *Rafflesioideae* are only known from Indomalesia, the other two tribes of that subfamily (*Cytineae* and *Apodantheae*) occur in America, Africa, the Mediterranean region (including Iran and Iraq), and SW Australia. The subfamily *Mitrastemoideae* has only one genus, *Mitrastema*, originally found in E and SE Asia, but later also recorded from Mexico, Guatemala, and Colombia (Meijer 1993).

HABITAT

All Malesian species are restricted to moist, evergreen, lowland or montane, primary or adjacent secondary forests.

1) With contributions by R.W.J.M. van der Ham, Leiden (palynology), and R. Hegnauer, Leiden (phytochemistry). Most original drawings are by Janis Atlee, Lexington, one by Herbert Lee, Tenom (Sabah). Photographs are from different sources as indicated. Inclusion of the colour plates was made possible through a substantial financial contribution by the author.

ECOLOGY

The ecology of *Rafflesiaceae* is of course closely interwoven with the host-parasite relationship, the chances of survival and the specific ecological requirements of the host plants, pollination efficiency, seed dispersal and dormancy, and germination chances. Between the production of about 100–150 seeds in a peppercorn-sized fruit of *Pilostyles* and a fist-size fruit of *Rafflesia* with several millions of seeds exists an enormous range of seed production per flower.

Mitrastema is most consistently reported as parasitizing the roots of *Fagaceae*: *Quercus, Lithocarpus, Trigonobalanus*, and *Castanopsis* and, if collectors' notes are accurate, occasionally adjacent tree roots of other families. All three genera of the tribe *Rafflesieae* (*Rhizanthes, Rafflesia, Sapria*) are obligate parasites of the genus *Tetrastigma* in *Vitaceae*. Where species names are mentioned in the treatment, they must be considered as preliminary, since identification of herbarium specimens is difficult and nomenclature uncertain.

Literature: Bänziger, H., Nat. Hist. Bull. Siam Soc. 39 (1991) 19–52; ibid. 43 (1995) 337–365.

TAXONOMY

Since Dumortier (1829) most systems of plant families of the world have treated *Rafflesiaceae* in a wide sense. Lindley (1836) and Richard (1838) considered *Cytinaceae* to be a separate family with *Pilostyles* as part of the *Rafflesiaceae* and the very closely related *Apodanthus* in the *Cytinaceae*. Van Tieghem (1890) elevated *Apodanthaceae* to the rank of family and Makino (1911) put his new genus *Mitrastema* in its own family. More recent accounts, as Thorne (1992), Beaman et al. (1992) and Meijer (1993) treat the family in a wide sense. Takhtajan et al. (1985) considered *Rafflesiaceae* sensu lato as a heterogeneous group, both macromorphologically and palynologically, and expressed the idea that the four tribes recognized by Harms (1935) deserve to be treated as separate families:

Rafflesiaceae: Rafflesia, Rhizanthes, Sapria
Apodanthaceae: Apodanthes, Pilostyles
Cytinaceae: Bdallophyton, Cytinus
Mitrastemaceae: Mitrastema.

Studies of ribosomal RNA of parasitic plants carried out by Dr Daniel Nickrent in Carbondale (University of South Illinois) are still preliminary but already support the removal of *Cytinaceae* from the *Rafflesiaceae* and ultimately may support the family system of Takhtajan et al. (1985). The ribosomal DNA data (Nickrent & Duff, in press) make it clear that the tribe *Cytineae* deserves to become a family at its own. Results on *Apodanthes* and *Pilostyles* are not yet available but it is quite possible also that they cannot easily be compared with the *Rafflesia* tribe (or family sensu stricto).

Solms-Laubach (1901: 7) warned not to rush to conclusions about the taxonomy and relationships of parasitic plants, which could hide their real ancestry in their strong reductions and adaptations required to survive as parasites. We can safely restrict ourselves

here to the tribe *Rafflesieae* and the subfamily *Mitrastemoideae* and leave it to future research as to how closely or distantly they might be related.

Literature: Beaman, R., et al., in: G. Ismael (ed.), Proc. Int. Conf. For. Biol. & Cons. Borneo (1992) 109. — Brown, R., Ann. Sc. Nat. 2, 1 (1834) 369–370; Trans. Linn. Soc. London 19 (1844) 221–239, 5 pl. — Dumortier, B.C.J., Anal. Fam. Pl. (1829) 14. — Harms, H., in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 243–281. — Lindley, J., Nat. Syst. Bot., ed. 2 (1836) 389–392. — Makino, T., Bot. Mag. Tokyo 25 (1911) 254–257, pl. 7. — Meijer, W., Rafflesiaceae, in: K. Kubitzki (ed.), Families & Genera of Vascular Plants, vol. 2: K. Kubitzki, J.G. Rohwer & V. Bittrich (eds.), Flow. Pl., Dicot. (1993) 557–563. — Nickrent, D.L. & R.J. Duff, Proc. 6th Parasitic Weed Symp. April 1996, Cordoba, Spain (in press). — Richard, A., Nouv. Elem. Bot., ed. 6 (1838) 1518–1520. — Solms-Laubach, H., in Engler & Prantl, Nat. Pflanzenfam. 3, 1 (1889) 274–282; in Engler, Pflanzenr. 5 (1901) 1–19, 13 illus. — Takhtajan, A.L., N. Meyer, R. & V.N. Kosenko, Bot. J. Leningrad 70 (1985) 153–162. — Thorne, R.F., Aliso 13 (1992) 365–389. — Van Tieghem, P.E.L., Traité Bot., ed. 2 (1890) 1577–1579.

PHYLOGENETIC AFFINITIES

As suggested before, considerations of this subject are still very speculative and depend on how natural the family in a wide sense really is. Takhtajan (1980) placed the two families *Hydnoraceae* and *Rafflesiaceae* in the order *Rafflesiales* in the superorder *Rafflesianae* (subclassis *Magnoliidae*). The closest relationship may well be with *Aristolochiaceae* which already Linnaeus (1753), Robert Brown (1821) and Solms-Laubach (1901) considered possible or likely. Nickrent & Duff (in press) in their preliminary work link *Hydnoraceae* with 'paleoherbs' like *Aristolochiaceae*. The position of *Rafflesiales* between *Santalales* and *Celastrales* in Cronquist's system (1981) might be at variance with the evidence from floral morphology and pollen morphology. As mentioned earlier Takhtajan (1985) proposed to raise all the tribes from the system by Harms (1935) to the rank of family, based on his studies of pollen structure. Thorne (1992), however, stuck to Takhtajan's family system of 1980 but ranked his *Rafflesianae* between *Nymphaeanae* and *Caryophyllanae*. The cladistic analysis of Beaman et al. (1992) was also based on Takhtajan's circumscription (1980) of the family and hinges on the selection of the most primitive genus and the most closely related family: *Hydnoraceae* or *Aristolochiaceae*. The old family circumscription as followed in this flora can only be maintained when reversals are assumed.

Literature: Beaman, R., et al., in: G. Ismael (ed.), Proc. Int. Conf. For. Biol. & Cons. Borneo (1992) 109. — Brown, R., Trans. Linn. Soc. London 13 (1821) 201–234, 8 pl. — Cronquist, A., Integr. System Class. Flow. Plants (1981) 703–704. — Harms, H., in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 243–281. — Linnaeus, C., Spec. Pl. (1753) 442. — Nickrent, D.L. & R.J. Duff, Proc. 6th Parasitic Weed Symp. April 1996, Cordoba, Spain (in press). — Solms-Laubach, H., in Engler, Pflanzenr. 5 (1901) 1–19, 13 illus. — Takhtajan, A.L., Bot. Rev. 46 (1980) 225–359. — Takhtajan, A.L., N. Meyer, R. & V.N.Kosenko, Bot. J. Leningrad 70 (1985) 153–162. — Thorne, R.F., Bot. Rev. 58 (1992) 225–348.

VEGETATIVE MORPHOLOGY AND ANATOMY

The vegetative parts are a kind of tissue mass often compared with fungal mycelia. The cells have remarkable large nuclei and form the so-called endophytic system within the

stems and roots of the host plants, especially inside the living bark close to the cambium of the host. From there, special strings (so-called sinkers) can penetrate through rays of the host into the deeper lying xylem, while these cell strings inside the host cambium in general keep pace with the secondary growth of the host. In *Pilostyles thurberi* the endophytic body stays at a uniform distance from the apical meristem of the host (Rutherford 1970), in the *Cytineae* generally near the ground level and in the *Rafflesieae* in the roots as well as high on stems, though in general close to the ground. When the host cambium is reactivated, it may succeed to put a xylem layer on top of the parasite tissues. In general the parasite can migrate through the rays into the new host tissues, as described by Forstmeier et al. (1983) for *Cytinus*.

The simple cell strings do not contain vascular tissues; in many genera these occur mainly in cell cushions from which flowering structures originate, connecting ultimately with the staminal or ovary structures.

Solms-Laubach (1869) described the situation in *Cytinus* where the parasite forms a kind of tissue sleeve between cambium and xylem of the *Cistus* host root. In a rhythmic way, parts of the parasite tissue are covered by xylem layers, apparently and for unknown reasons turning the cambium activity off from time to time. The resulting more mature closed cylinder sleeve of the parasite consists of a cambium and two surrounding layers of tissue: an inner medullary and outer cortical plate. In the latter many irregular weak vascular bundles occur. Flowering structures originate inside swollen parenchyma tissues and cause gall-like growth above connections with the vascular bundles of the host plant, in general at least 2–3 years after the first infection of the host. The host tissues are filled with starch at this place except in a few cell layers close to the parasite tissue. These and similar situations were observed by Cartellieri (1926) in *Rhizanthes*, Brown (1912) in *Rafflesia manillana*, Haak (1889), Schaar (1898) and Hunziker (1920) in *Rafflesia patma*, Endriss (1902) in *Pilostyles ingae*, Rutherford (1970) in *Pilostyles thurberi* and Meijer & Behnke (unpubl.) in *Rhizanthes*, while the old classical study by Solms-Laubach (1875) is still of value. If the family is polyphyletic we are dealing here with remarkable convergences in growth morphology.

Kuijt et al. (1985) discovered sieve elements in the endophytic body of *Pilostyles thurberi*, apparently in a discontinuous system which they considered to be a vestigial cell type. In older studies such elements were in general overlooked.

Weak vascular tissues are reported from the endophytic bodies of species of *Pilostyles*. Floral tissue cushions contain rings of concentric vascular bundles in *Rafflesia* and *Rhizanthes*.

Most of the tissues are parenchymatous and these cells also never contain starch. In all genera the parenchymatous tissues are rich in tannins.

Stomata are known from scales of *Pilostyles* and *Cytinus* and also from *Rafflesia* and *Rhizanthes* (see Cammerloher 1920). Glandular hairs are known from the bracts of *Cytinus* and also in some species from the perigone. The function of the so-called ramenta, the outgrowths inside the flower tubes of species of *Rafflesia* and from the upper part of the diaphragm of *Sapria* is still unknown; their different forms have diagnostic taxonom-

ic value (Winkler 1927). The osmophoric and nectarial structures of the family still need more comparative anatomical studies.

Literature: Brown, W. H., Philipp. J. Sc., Bot. 7 (1912) 209–224, pl. 12–21. — Cammerloher, H., Oesterr. Bot. Zeitschr. 69 (1920) 153–164, t. 3. — Cartellieri, E. von, Bot. Archiv 14 (1926) 284–311, 7 pl. — Endriss, W., Flora, 91, Erg. Band (1902) 209–236, t. 20. — Forstmeier, L., F. Weberling & H.C. Weber, Beitr. Biol. Pflanzen 58 (1983) 299–312. — Haak, J., Observ. Rafflesias (1889) 14 pp. — Hunziker, J., PhD Thesis Freiburg (1920). — Kuijt, J., D. Bray & L.R. Olson, Canad. J. Bot. 63 (1985) 1231–1240. — Rutherford, R.J., Aliso 7 (1970) 263–288. — Schaar, F., Sitzungsber. K. Akad. Wiss. Wien, Math.-Naturw. Kl. 107 (1898) 1039–1056. — Solms-Laubach, H., Bot. Zeitung 27 (1869) 185–190; Abh. Naturf. Ges. Halle, 13, 3 (1875) 40 pp., t. 24–27. — Winkler, H., Planta 4 (1927) 1–97, t. 1.

FLOWER MORPHOLOGY

Only in the genus *Bdallophyton* do the flowering structures (inflorescences) have a well developed long axis. In all other genera they are more or less fascicles or very short uniflowered shoots, surrounded by a few whorls of scaly dark brown or blackish leaves. In *Rafflesia* and *Rhizanthes* there are in general 3 whorls of 5 scales (bracts), in *Pilostyles* the whorls are 3–6-merous. *Apodanthes* has a regular structure of 2 outer bracts, 4 calyx-like bracts followed by 4 perigone lobes and an ovary with 4 placentas. Only in the tribus *Cytineae* inflorescences are developed like racemes, spikes or umbels, sometimes with bracts and bracteoles.

Flowers are in general unisexual. In *Rhizanthes zippelii* unisexual flowers occur besides bisexual ones. *Bdallophyton oxylepis* has bisexual flowers and *B. americanum* unisexual ones on different plants; *Mitrastema* is always bisexual and protandrous.

Perigones can be partly tubular at their bases and the lobes are imbricate (*Rafflesia*) or valvate (*Rhizanthes*). *Rafflesia* and *Sapria* possess as unique organ the diaphragma. Staminal structures always have the thecae interconnected in a ring like in *Hydnoraceae*, though never in phalanges, and are in various ways connected with the central column. In some cases in *Pilostyles* they occur in 2–4 rings. The detailed anatomy of the anthers in various genera shows also some variation (see Fig. 1).

Literature: Koorders, S.H., Bot. Overz. Raffles. Ned.-Indië (1918) 206–215. — Meijer, W., in: K. Kubitzki (ed.), Families & Genera of Vascular Plants, vol. 2: K. Kubitzki, J.G. Rohwer & V. Bittrich (eds.), Flow. Pl., Dicot. (1993) 557–563.

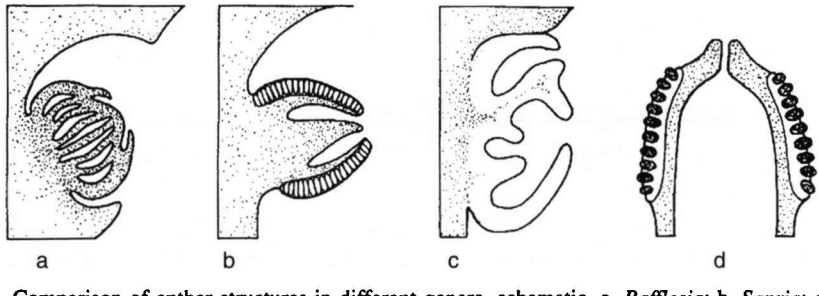

Fig. 1. Comparison of anther structures in different genera, schematic. a. *Rafflesia*; b. *Sapria*; c. *Rhizanthes*; d. *Mitrastema*. Drawing Janis Atlee.

PALYNOLOGY
(R.W.J.M. van der Ham)

The most detailed account of *Rafflesiaceae* pollen is that of Takhtajan et al. (1985), which includes light and electron microscopic data of 25 species belonging to 7 genera. Others deal with one or a few species only. Straka (1978), Straka & Friedrich (1984) and Valdes et al. (1987) provide pollen descriptions with light and scanning electron micrographs of a few species of the most diverse genus *Cytinus*.

Pollen of the four tribes, as recognised by Harms (1935), is so different that it cannot be easily covered in a single description. Pollen grains of the *Rafflesieae* (*Rafflesia*, *Rhizanthes*, *Sapria*) are subspherical to ellipsoidal, 12–21 µm large monads, with one distal pore or short colpus. The exine consists of a lamellate endexine (2–4 sublayers) and a loosely attached, sporopollininous perine-like outer layer. Pollen of *Rafflesia arnoldii* also has a homogeneous ectexine. The ornamentation is finely to very coarsely rugulate-verrucate.

Pollen grains of the *Apodantheae* (*Pilostyles*; pollen of *Apodanthes* and *Berlinianche* still unknown) are prolate (P × E = 18–28 × 10–20 µm), tricolpate monads. The colpi are long and narrow. The exine consists of a homogeneous ectexine and an endexine that is often lamellate in its outer part. Locally the ectexine may be differentiated into tectum, columellate infratectum and foot layer. The ornamentation is ± psilate.

Pollen grains of the *Cytineae* (*Cytinus*, *Bdallophyton*) are monads (*Cytinus*, *Bdallophyton*), or they are united in tetragonal, rhomboidal or tetrahedral, calymmate or acalymmate tetrads or, sometimes, dyads (*Cytinus*). The grains are subspherical to ellipsoidal, subiso- to heteropolar, 11–24 µm large, with 2–4 ± equatorial pori or short colpi (*Cytinus*), or (2) 3–4 long meridional colpi (*Bdallophyton*). The exine consists of a tectum, a distinct columellate infratectum and a nexine. The endexine is very thin, and recognisable only in the apertural areas. *Cytinus* pollen is sometimes semi- or intectate. The ornamentation is verrucate, perforate or ± reticulate in *Cytinus*, and perforate in *Bdallophyton*.

Pollen grains of the *Mitrastemoneae* are triangular-ellipsoidal, 25 –28 µm large monads, usually with 3 equatorial(?) pores. The exine mainly consists of endexine, which is lamellate near the apertures. The ectexine is represented by small isolated verrucae. The ornamentation is psilate to scabrate.

The heterogeneity of *Rafflesiaceae* pollen led Takhtajan et al. (1985) to the concept that the family should be split into four natural families: *Rafflesiaceae* sensu stricto, *Apodanthaceae*, *Cytinaceae* and *Mitrastemaceae* (see also p. 2). They did not indicate if these families form a monophyletic taxon. The single distal (monosulcate, ulcerate) aperture and the throughout lamellate endexine of the pollen of the *Rafflesieae* – primitive features within the dicotelydons – suggest that this group belongs to the subclass *Magnoliidae*, near the *Aristolochiaceae* (Takhtajan et al. 1985). With respect to the monophyly of the *Rafflesiaceae* sensu lato, it is important to determine whether the (2-) 3- (4-)porate and -colpate pollen types of the other tribes are 'monosulcate-derived' or 'tricolpate-derived' (Walker & Doyle 1975), and also if the monosulcate/ulcerate aperture type of the *Rafflesieae* represents the original, primitive state of the aperture in *Magnoliidae* pollen.

References: Harms, H., in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 243 – 281. — Straka, H., Pollen et Spores 20 (1978) 162–163. — Straka, H. & B. Friedrich, Trop. Subtrop. Pflanzenwelt 51 (1984) 545–546. — Takhtajan, A.L., N.R. Meyer & V.N. Kosenko, Bot. J. Leningrad. 70 (1985) 153–162. — Valdes, B., M.J. Díez & I. Fernández, Atlas polinico de Andalucía Occidental (1987). — Walker, J.W. & J.A. Doyle, Ann. Missouri Bot. Gard. 62 (1975) 664–723.

POLLINATION

The foetid smell of the flowers of *Rafflesia* attracts carrion-flies of the genus *Lucilia* (Docters van Leeuwen 1929; Ross in Meijer 1985; Beaman et al. 1988; Bänziger 1991). The smell is produced by fresh flowers, especially during sunny warm periods of the day. Beaman et al. suggested they observed green flies in action in *Rafflesia* at the upper part of the gullies in the column leading to the anther cavities between rows of hairs (Meijer 1985). The actual act of pollination is well illustrated by Bänziger (1991), see Fig. 2. Still nobody has fully documented with a video camera what the flies do: laying eggs, collecting nectar (Haak 1885) or just using the carpet of ramentae as a mating ground (as insects do inside the odorous inflorescences of aroids: Croat, verbal comm.). The flies carry the pollen on their backs but have not been observed to use it as food. The actual source area (osmophore) of the bad odour is also still not yet known. Bänziger (1991) suggested from his own observations that the smell originates from the perigone lobes. Maybe the stomata described by Cammerloher (1920) have a function after all.

Douglas Warren Stevens noticed during his exploration of Nicaragua a faint smell from the flowers in *Bdallophyton americanum* (verbal comm.) and Rutherford (1966) reported this also from the masses of flowers of *Pilostyles thurberi*, both genera which like *Cytinus* and *Mitrastemon* also produce nectar. Honeyeater birds use flowers of *Mitrastemon* in New Guinea as nectar source (Beehler 1994).

Bänziger (1995: 352–356) gave interesting new data on solidification of the liquid pollen of *Rhizanthes* on the back of pollinating insects and reliquefying by profuse stigmatic fluid and viability over a period of 3 weeks. He also gave details with more recent names of the pollinating carrion flies now classified as *Calliphoridae*.

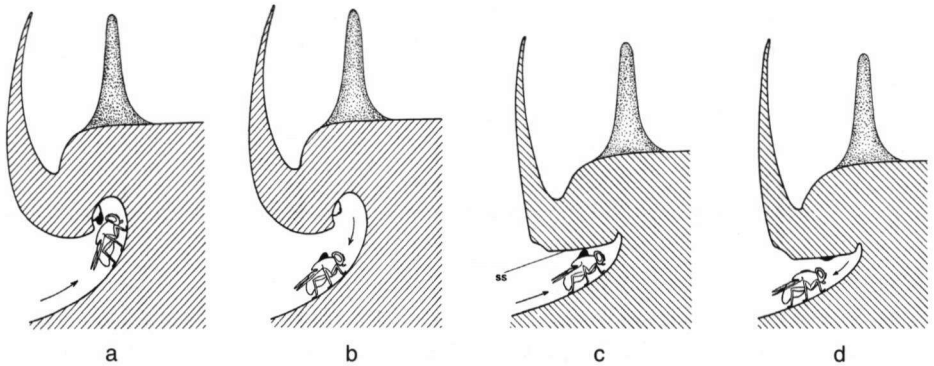

Fig. 2. Schematic pictures of flies picking up pollen in a male flower of *Rafflesia kerrii* (a, b) and striking it off on the stigma of a female flower (c, d). ss: stigmatic surface. Reproduced with permission from Bänziger (1991).

References: Bänziger, H., Nat. Hist. Bull. Siam Soc. 39 (1991) 19–52; ibid. 43 (1995) 337–365. — Beaman, R., et al., Amer. J. Bot. 75 (1988) 1148–1162. — Beehler, B.M., Biotropica 26 (1994) 459–461. — Cammerloher, H., Oesterr. Bot. Zeitschr. 69 (1920) 153–164, t. 3. — Docters van Leeuwen, W.J., Trop. Natuur 18 (1929) 43–45. — Haak, J., Weekbl. Pharmacie 3 (1885) 19 pp., 2 pl. — Meijer, W., Nat. Geogr. 168 (1985) 136–140. — Rutherford, R.J., PhD Thesis Claremont Grad. School, USA (1966).

LIFE CYCLE

If we assume that the species of *Rafflesia* do not vary much in their life cycles we can reconstruct from data supplied by Teijsmann (1856a, b, 1858), Docters van Leeuwen (1929), Meijer (1958 and recent unpublished observations) that the total life cycle in that genus from seed to seed is about 3–4.5 years. New experiments started in Bogor and in temperate greenhouses in 1991 with seeds of *R. gadutensis* from West Sumatra, so far have not produced results. The life cycles of other genera of this family in Malesia are still incompletely known, except that Bänziger (1995) observed for buds of *Rhizanthes lowii* (*Rh. zippelii* sensu Bänziger) that it took an estimated 200–255 days from the point of breaking through the host tissue at a circumference of 3.7 to 4.1 cm to opening of the flower.

References: Bänziger, H., Nat. Hist. Bull. Siam Soc. 43 (1995) 337–365. — Docters van Leeuwen, W.J., Trop. Natuur 18 (1929) 43–45. — Meijer, W., Ann. Bogor. 3 (1958) 33–44. — Teijsmann, J.E., Nat. Tijds. Ned. Indië 12 (1856a) 279–281; Hook. J. Bot. & Kew Gard. Misc. 8 (1856b) 371–374; Ann. Hortic. Bot., Fl. Jard. Roy. Pays-Bas (1858) 27–30.

FRUITS AND EMBRYOLOGY

Field observations in 1981 and 1983 in the Ulu Gadut area near Padang, West Sumatra have shown that ripening of fruits of *Rafflesia gadutensis* takes about 8 months. Two fruits were monitored for periods of 6–7 months and the eldest had ripe seeds in February 1984. Meijer's guide Satar, who was monitoring this fruit below his hut, mentioned that it was visited by a 'tupai kuning' (most likely a tree shrew), the same species which was eating his young chickens. In Sumatra as well as Borneo we noticed male buds being opened by squirrels or/and tree shrews and it looks as if one shrew sitting on the exit of such a vandalized bud was captured on the lens on Kinabalu near Poring; see Attenborough (1995). It sits on a bud not at the entrance of a flower as the legend in the book asserts. The holes made are too small for most squirrels.

From a very obscure report by R.H.C.C. Scheffer in a letter to Solms-Laubach [cited in Solms-Laubach (1875: 27)] it might appear that actual pollination is not necessary for fruit set. Scheffer wrote to Solms (translated): "Only one of the buds made it into a flower, only 3 years after the inoculation. Notwithstanding this was a female one, and without having a male flower nearby it still developed seeds. These were used to infect another plant of *Cissus scariosa* [= *Tetrastigma leucostaphylum*] and this was successful."

Solms asserts that Scheffer suspected that the rudimentary anthers might have produced some pollen. That is very unlikely. Meijer's unpublished field observations showed that unfertilized female flowers, several months after flowering, had produced no seeds with embryos. Ovaries with very little pollination may be stimulated to grow

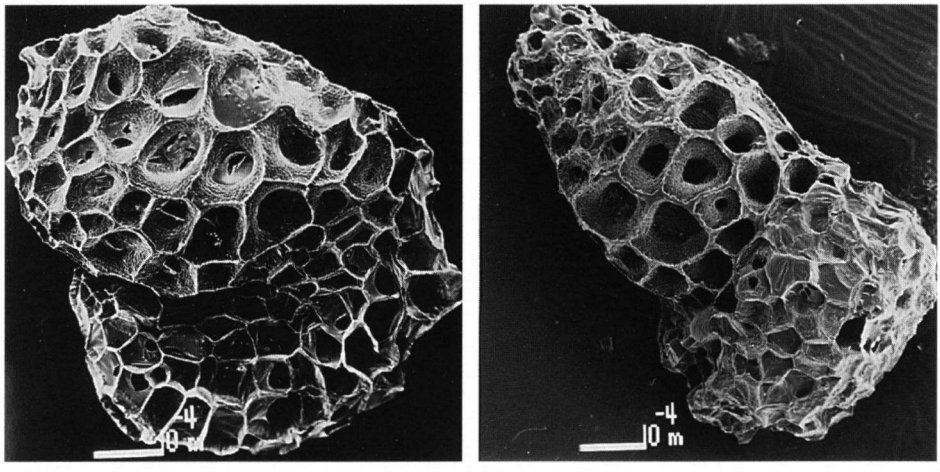

Fig. 3. Mature seeds of *Rafflesia rochussenii* Teijsm. & Binn. (left) and *Rhizanthes zippelii* (Blume) Spach (right). Scanning electron micrographs F. Bouman, courtesy Hugo de Vries-Laboratorium, University of Amsterdam.

into fruits, but they can be full of seeds without embryos as observed from a fruit of *Rafflesia keithii* outside the Kinabalu National Park, August 1993 (seeds tested by F. Bouman, Amsterdam). Possibly there were other flowers of *Rafflesia* open in the garden or on Mount Salak about 120 years ago, to account for Scheffer's observations. Real parthenocarpy of *Rafflesia* has never been proven.

Ovule and seed development stages have been studied for *Rafflesia* and *Rhizanthes* (Solms-Laubach 1898; Ernst & Schmid 1913). Pollen tetrads form according to the succedaneous system; the tapetum of anthers consists of 2 or 3 layers of cells. The stigma is in *Rafflesia* and *Rhizanthes* situated in a ring around the rim of the column disk, often more or less papillose; the ovary shows in these genera a maze of placental plates which fill the ovary cavity. For the development of the embryosac see Ernst & Schmid (1913) and Olah (1960). The outer integument is reduced. Ovaries grow into berry-like fruits, with whitish pulpa around the seeds. The seeds (Fig. 3) are small and with hard scales [see Harms (1935: 255) and Bouman & Meijer (1994)]. *Rafflesia patma* has a 2-cell suspensor and an embryo consisting of 3–5 layers of 2–4 cells, often only 6 cells in total. Endosperm is nuclear and consists of 30–40 cells in *R. patma*. Endosperm and embryo mostly contain oil, see also Schuerhoff (1926: 526). *Mitrastema* also has cellular endosperm, but ovules with only one integument.

References: Attenborough, D., The private life of Plants (1995). — Bouman, F. & W. Meijer, Pl. Syst. Evol. 193 (1994) 187–212. — Ernst, A. & E. Schmid, Ann. Jard. Bot. Buitenzorg II, 12 (1913) 1–58, t. 1–8. — Harms, H., in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 243–281. — Olah, L.V., Bull. Torrey Bot. Club 87 (1960) 406–416. — Schuerhoff, P.N., Zytol. Blütenpfl. (1926). — Solms-Laubach, H., Abh. Naturf. Ges. Halle 13, 3 (1875) 40 pp., t. 24–27; Ann. Jard. Bot. Buitenzorg 9 (1891) 184–246, 28 pl.; ibid., Suppl. 2 (1898) 11.

DISPERSAL

Watanabe (1933, 1936) assumed long range seed dispersal of *Mitrastema* by birds. Observations of jungle walkers working for Meijer (1958, 1983) at the sites of *Rafflesia* in West Sumatra showed that ground squirrels and tree shrews like to eat the contents of the white pulpy ripe fruits of these plants. These observations have been confirmed now by Emmons, Jamili Nais and Ali Briun (1991) and documented with colour photographs from a hide erected in August 1989 near a fruit of *Rafflesia keithii* on Mt Kinabalu. The fruits of *Rhizanthes* also have white pulp, but they are hidden under the old perigones and predation has never been observed yet.

In analogy with other root and stem parasitic plants it is assumed that only disturbance and damage to the organs of the host can deliver the signal for seeds in contact with them to germinate (Bouman & Meijer 1994).

References: Bouman, F. & W. Meijer, Pl. Syst. Evol. 193 (1994) 187–212. — Emmons, L., et al., Biotropica 23 (1991) 197–199. — Meijer, W., Ann. Bogor. 3 (1958) 33–44, fig.; Essays on Rafflesiaceae (1983) 1–20. — Watanabe, K., Bot. Mag. Tokyo 47 (1933) 798–805; J. Jap. Bot. 12 (1936) 603–618.

PHYTOCHEMISTRY

(R. Hegnauer)

This mainly tropical family of parasitic plants is badly known at present from a chemical point of view (see Hegnauer 1973, 1990). *Cytinus hypocistis* yielded isoterchebin, an ellagitannin, as its yellow pigment and pelargonidin 3-galactoside and petunidin 3-glucoside as red flower pigments. The sole crystalline compound isolated from acetone extracts of *Psilostyles thurberi* turned out to be sucrose. Pollination biology of *Rafflesiaceae* is still poorly known. Recent observations with *Rafflesia pricei* suggest that optical and olfactory mimicry may offer the clue. Flower pigments and odorous principles emanated from flowers attract carrion-flies; they seem not to be compensated for their pollination activities by nurture or suitable breeding sites. Most authors are convinced that *Rafflesiaceae* belong to or are affiliated with *Polycarpicae* sensu Wettstein. However, synthesis and accumulation of ellagitannins do not favour such an assumption, because polymeric proanthocyanidins (i.e. 'condensed tannins') are the characteristic tannin-like metabolites of *Polycarpicae*. In this respect *Rafflesiaceae* are similar to *Nymphaeaceae* s.str. which produce ellagitannins and possibly *Cabombaceae* which produce gallic acid and probably gallotannins. Therefore it is noteworthy that Takhtajan (1980) has *Aristolochiales*, *Rafflesiales*, *Nymphaeales* (*Cabombaceae*, *Nymphaeaceae* s.str. and *Ceratophyllaceae*) and *Nelumbonales* as numbers 5–8 in his subclass *Magnoliidae*, and that in Thorne's (1992) classification *Aristolochiaceae* are incorporated in *Magnolianae–Magnoliales–Magnoliidae* and the superorders *Nymphaeanae* and *Rafflesianae* immediately follow *Magnolianae*. *Nelumbonales* and *Ceratophyllales* are treated by Thorne as orders of *Magnolianae*. Synthesis and accumulation of gallo- and ellagitannins may have evolved in a number of taxa now considered as outgroups of true polycarps.

References: Hegnauer, R., Chemotaxonomie der Pflanzen 6 (1973) 9; 9 (1990) 314–315. — Takhtajan, A.L., Outline of the classification of flowering plants (*Magnoliophyta*), Bot. Rev. 46 (1980) 225–359. — Thorne, R.F., Classification and geography of flowering plants, Bot. Rev. 58 (1992) 225–348.

KEY TO THE GENERA

1a. Ovary superior, staminal structure a tube surrounding the pistil with a series of anthers above each other. Host plants in general *Fagaceae* .... **Mitrastema** *(p. 11)*
b. Ovary inferior or half-inferior, staminal structures different. Host plants species of *Tetrastigma* (*Vitaceae*) 2
2a. Mature flower buds oblong. Perigone without diaphragm, lobes 16–18, valvate, ending in bayonets (elongate stiff pointed appendages), which are hidden in a cavity at apex of the column while flowers are in the bud stage . **Rhizanthes** *(p. 37)*
b. Mature buds more or less globular. Perigone with a diaphragm, the lobes imbricate, 5–10 3
3a. Perigone lobes 5; ramenta only inside the flower tube ..... **Rafflesia** *(p. 13)*
b. Perigone lobes 10; ramenta on top of the diaphragm ... **Sapria** (Continental Asia)

MITRASTEMA

Mitrastema Makino, Bot. Mag. Tokyo 23 (1909) 326 ('*Mitrastemma*'). — *Mitrastemon* Makino, Bot. Mag. Tokyo 25 (1911) 225, orth. mut., nom. inval.; Jochems, Rec. Trav. Bot. Néerl. 259 (1928) 203; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 274; Yamamoto, Bot. Mag. Tokyo 50 (1936) 539; Watanabe, J. Jap. Bot. 13 (1937) 154; Matuda, Bull. Torrey Bot. Club 74 (1947) 133; Meijer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 560; Meijer & Veldkamp, Blumea 38 (1993) 221–229. — Type species: *Mitrastema yamamotoi* Makino ('*Mitrastemma*').

Chlorophyll-less endoparasites with fungus-like endophytic body. Stems unbranched. *Leaves* scale-like, decussate. *Flowers* solitary, terminal, bisexual. *Perianth* much reduced, collar-shaped. *Stamens* numerous, completely connate into a tube, below the sterile apical part with several vertical series of rings of c. 10 anthers each; pollen dicolpate, with reduced ectexine. *Ovary* superior, 1-locular, ovules numerous, anatropous, unitegmic. *Fruit* a slightly woody, berry-like capsule, horizontally dehiscing. *Seeds* sticky, testa hard. — **Fig. 4, 5.**

Distribution — Two species, one in Asia, from Japan to Taiwan, Yunnan, Bhutan, Assam, Indo-China, and *Malesia:* Borneo, Sumatra and New Guinea; a second, very closely related species (?) from Chiapas (Mexico) to Alta Vera Paz (Guatemala) and Antioquia (W Colombia).

Habitat — In montane oak-chestnut forests, altitude 1400–2000 m.

Ecology — The Asian species parasitic on roots of *Fagaceae*, probably the American species too. Pollination by insects and birds, seed dispersal most likely by birds and small mammals.

Notes — 1. According to Matsuura, J. Fac. Sc. Hokkaido Imp. Univ. V, Bot. 3 (1935) 189, and Watanabe, J. Jap. Bot. 12 (1936) 769, f. 26P, the chromosome number is n = 20.

2. About the orthography of the genus name, see Meijer & Veldkamp, l.c.

Mitrastema yamamotoi Makino

Mitrastema yamamotoi Makino, Bot. Mag. Tokyo 23 (1909) 326, fig.; P. Royen, Nova Guinea, Bot. 14 (1963) 243–245, pl. 17; Hansen, Bot. Tidsskr. 67 (1972) 149; in Fl. Camb., Laos & Vietnam 64 (1973) 62, t. 9; Tang Shui Liu & Ming You Lai in Fl. Taiwan 2 (1976) 582, t. 414; Meijer & Veldkamp, Blumea 38 (1993) 227. — Syntypes: *Tashiro s. n., Bando s. n., Yamamoto s. n.* (TI holo), Japan, Kyushu.

Mitrastemon sumatranum Nakai, Icon. Pl. As. Or. 4 (1941) 338, t. 113 ('*sumatranus*'). — Type: *Jochems s. n.* (TI holo), Sumatra, Karo Mts.

For more complete synonymy and references, see Meijer & Veldkamp, l. c.

Plants about 2.5–15 cm long and up to 3 cm in diameter. Basal part a corky pustular cupule, up to c. 2 cm high and in diameter, the margin an irregularly low lobed rim; stems 5–15 mm diam. *Leaves* (also called bracts or scales) in 3–4(–7) decussate whorls, increasing in length from the base of the plant upwards, broadly to narrowly ovate, at apex blunt-rounded, (4–)10–20(–28) by (5–)10–15(–25) mm, cream (turning ebony) coloured with brown spots, the lowest often purplish brown. *Flowers* up to 20 mm long, with a foetid smell. *Perigone* 5–10 by 6–17 mm, truncate or slightly 4-lobed. *Staminal tube* tubular, wide and globose in the basal part, 14–20 mm long, the minute anthers in a 2–5 mm broad ring in the upper part, the whole collar early caducous. *Ovary* ellipsoid, c. 8 by 3 mm, style ovoid-ellipsoid, 2–8 by 3–6 mm, stigma 2–5 by 4–6 mm; 8–15 radial placentas. *Fruit* up to c. 20 by 10 mm, opening along a horizontal ring about halfway. *Seeds* c. 0.25 mm diameter, with a small funicle, yellowish or dark brown. — **Fig. 4, 5.**

Distribution — India, Thailand, Cambodia, Vietnam, China (Yunnan), Japan, Taiwan; *Malesia:* Sumatra (Aceh, East Coast), Borneo (Sabah: Mt Kinabalu; Sarawak: 4th Division), Papua New Guinea (W and E Highlands, Morobe, Milne Bay Provinces).

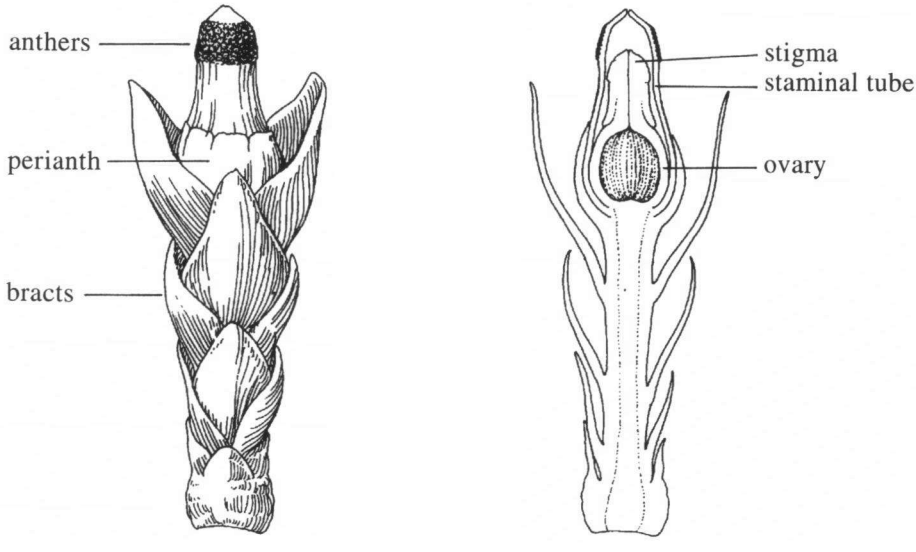

Fig. 4. *Mitrastema yamamotoi* Makino. Full open flower, habit and length section, with indication of flower parts. True size up to 15 cm high. Drawing by Janis Atlee after the type description by Makino.

Fig. 5. *Mitrastema yamamotoi* Makino. Dried flower on host. Sumatra, Berastagi, coll. by A. Stomps Photo by F. D. Boesewinkel, Amsterdam.

Habitat — Montane oak forests, at altitudes of 1400 to 2000 m.

Ecology — In Malesia *Mitrastema yamamotoi* is in general reported as a root parasite of *Fagaceae: Castanopsis, Lithocarpus, Quercus, Trigonobalanus* [Akuzawa, Paras. Pl. Magaz. 13 / 4 (1985) 23], but also on species of other families. Flowering is reported on Mt Kinabalu around April, the fruits ripening in about 4 months [Akuzawa, Paras. Pl. Magaz. 15 / 1 (1986) 26].

RAFFLESIA

Rafflesia R. Br., Trans. Linn. Soc. 13 (June 1821) 201; Jack, Appendix Descr. Mal. Pl. 1 (July 1821); Jack ex Hook., Comp. Bot. Mag. 1 (1835) 259, pl. 14; R. Br., Trans. Linn. Soc. 19 (1844) 221; Solms-Laubach in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1889) 279; in Engl., Pflanzenr. 5 (1901) 8; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 259; Meijer, Blumea 30 (1984) 209; in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 561. — Type species: *Rafflesia arnoldii* R. Br.

Parasitic plants, endophytic body growing like a thallus inside the woody stems and roots of species of *Tetrastigma* (*Vitaceae*). *Flower buds* sessile, first protruding as a corky swelling with hexagonal patches, the corky base remaining as a cup-shaped body (cupule) below the scales on the flowering sessile shoot. *Scales* (bracts) in a series of 3 whorls of 5 scales, imbricate, at first appearance white, but turning black or dark brown

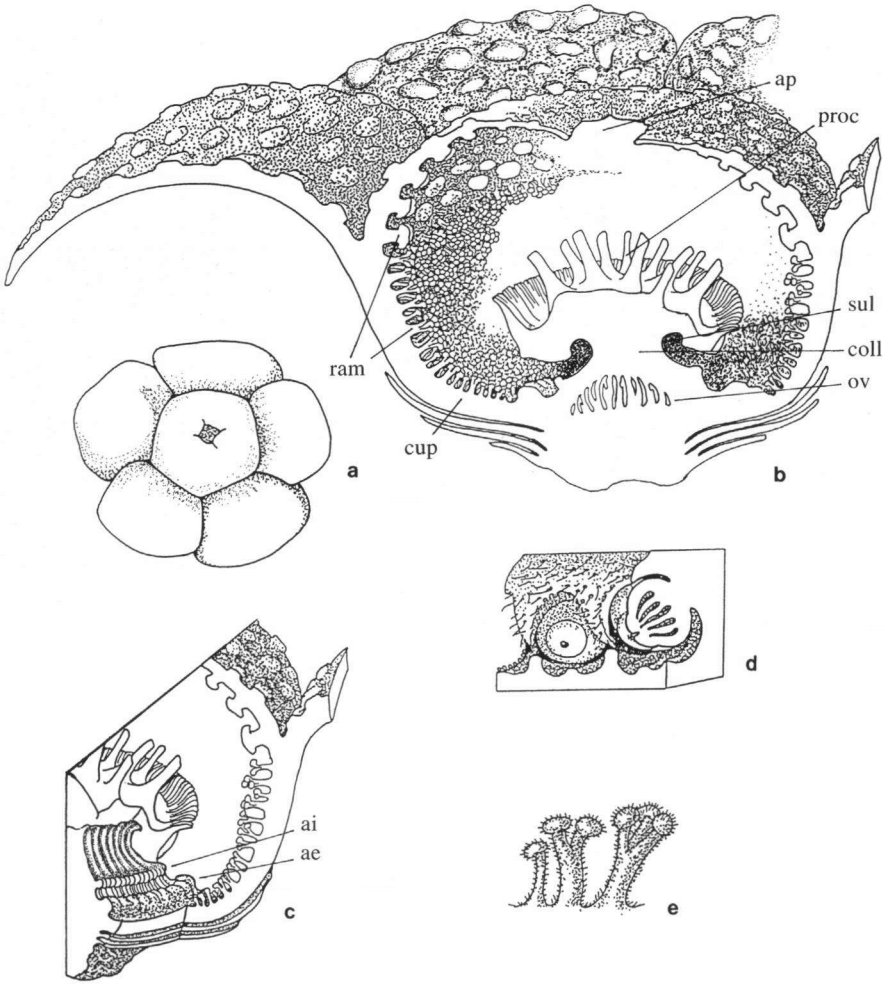

Fig. 6. *Rafflesia micropylora* Meijer. a. Flower with the small aperture in the diaphragm clearly showing; b. female flower, halved lengthwise, showing central column (ap: aperture in diaphragm; coll: collum, neck of column; cup: cupula, perigone tube; ov: ovary; proc: processi on apex of disc; ram: ramenta on inside of cupula and diaphragm; sul: sulcus under disc); c. side view of the column of a female flower showing outer and inner annulus (ae: annulus exterior, ai: annulus interior); d. section through male flowers, anther in longitudinal section and seen from lower side of the overhang of the 'corona' of the disc towards the sulcus; e. details of ramenta, often branched and with swollen apices. Drawings by Janis Atlee (a, b, d, e) and Herbert Lee (c), made from colour slides by W. J. de Wilde and drawings from BO.

after exposure, with prominent veins, inner gradually larger. *Flowers* (see Fig. 6) unisexual, female ones with rudiments of anthers. *Perigone lobes* 5, imbricate, reddish, often with white warts, inserted around an annular, horizontal, pentagonal, central diaphragm which has a more or less round opening (orifice) in the centre (see Fig. 7, 8).

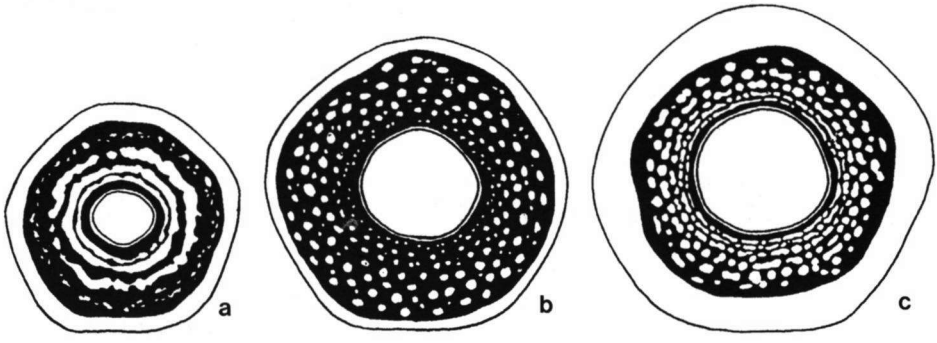

Fig. 7. *Rafflesia* spp. Semidiagrammatic representation of the diaphragms of: a. *Rafflesia hasseltii* (4 concentric rings, not of warts but at same level as surrounding tissue), b. *Rafflesia kerrii* (7 concentric rings of very small white warts), and c. *Rafflesia keithii* (5 concentric rings of white warts). Drawing by Janis Atlee.

Base of perigone tube and adjacent zone of diaphragm (or the entire diaphragm) covered with variably shaped ramenta inside (see Fig. 9). *Central column* at apex widened into a disk, often with processes, below this narrowed into the neck and at the base widened and surrounded by the 'annulus interior' above a sulcus, the base of the flower tube often thickened into an 'annulus exterior' which can be almost or totally obsolete. *Anthers* with one apical pore, sessile, situated around the overhanging rim of the column. *Ovary* 1-locular with many placentas. *Fruit* berry-like. *Seeds* thick-walled, c. 1 mm long and with a shorter appendage. — **Fig. 6–9, Plates 1–4.**

Distribution — About 13 species from the Kra Isthmus of Thailand through *West Malesia*, including Luzon and Mindanao in the Philippines. Possibly formerly also in Bali.

Habitat — In primary and secondary forest, the host *Tetrastigma* species prefer to grow in rich alluvial or limestone derived soils. As a result they never occur in areas with *Gleichenia* thickets. Moreover they are restricted to altitudes below about 2000 m. The highest reported *Rafflesia* is the site on Mt Leuser where Van Steenis found *R. rochussenii* at 1800 m. Most of the known localities are around 1000 m or lower. That may be the reason *Rafflesia* is now very rare on the rather denuded lower mountain slopes of West Java.

Some of the best *Rafflesia* and *Rhizanthes* sites are found outside old primary forests since *Tetrastigma* species germinate best in open disturbed soils from the seeds dispersed by birds or small mammals. How well the parasites can survive in severely cut back climbers is still unknown, but this can now be checked at some sites where silvicultural operations have damaged populations.

Ecology — Always parasitic on the trailing stems and/or roots of some species of *Tetrastigma* (*Vitaceae*).

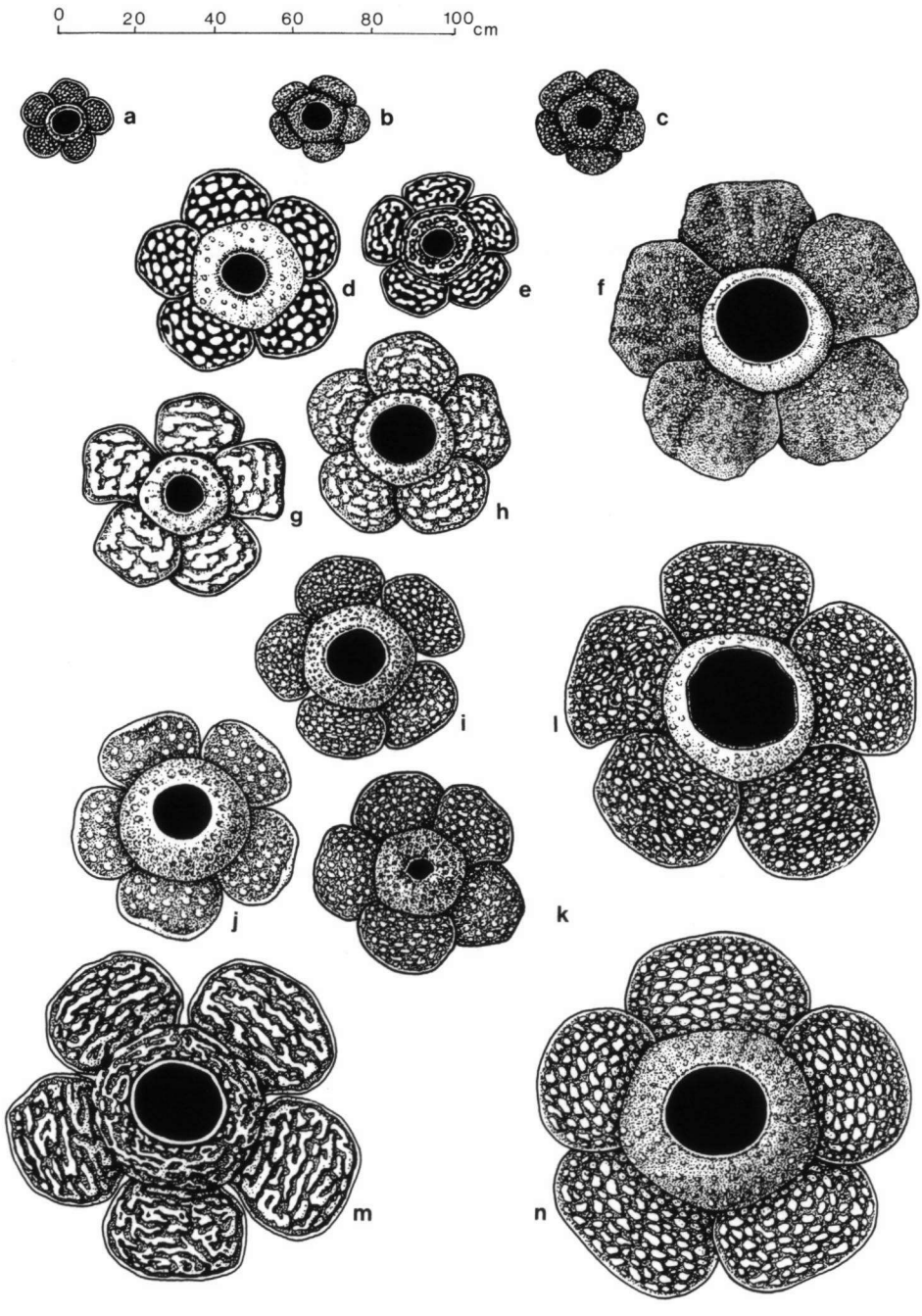

Fig. 8. *Rafflesia*. Fully open flowers. For each species a flower of average size is pictured from above. a: *R. manillana*, b: *R. rochussenii*, c: *R. tengku-adlinii*, d: *R. cantleyi*, e: *R. pricei*, f: *R. kerrii*, g: *R. hasseltii*, h. *R. gadutensis*, i: *R. patma*, j: *R. tuan-mudae*, k: *R. micropylora*, l: *R. keithii*, m: *R. schadenbergiana*, n: *R. arnoldii*. Drawn by Janis Atlee, from different sources in archives W. Meijer (MO).

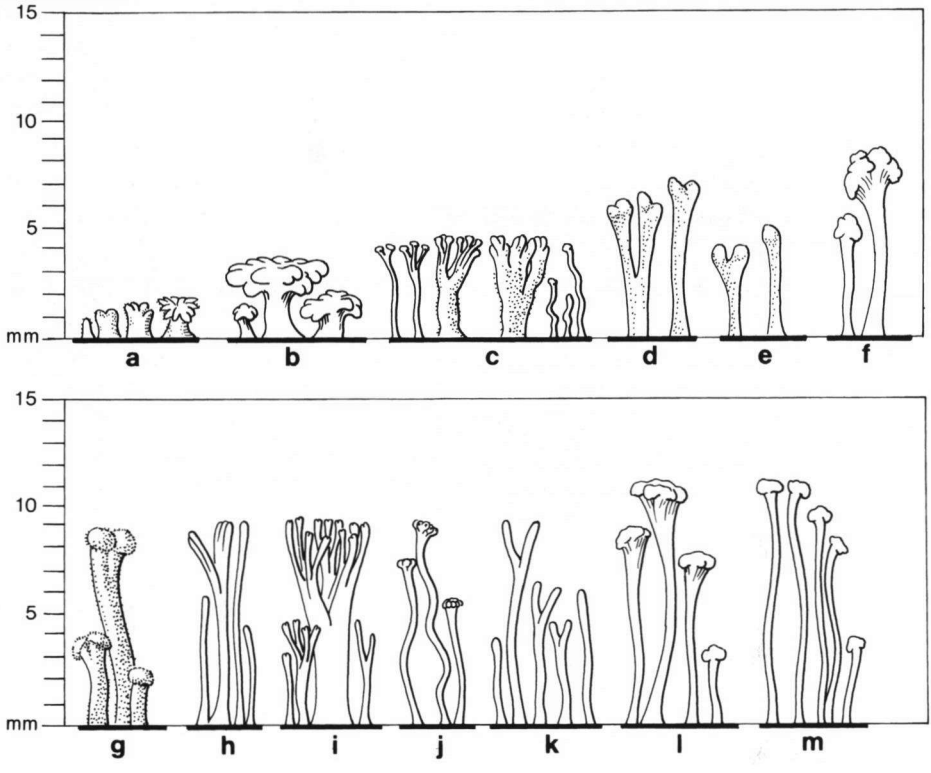

Fig. 9. *Rafflesia*. Ramenta from inside of perigone tube from 13 species, drawn on scale. a: *R. patma*, b: *R. manillana*, c: *R. tengku-adlinii*, d: *R. pricei*, e: *R. keithii*, f: *R. gadutensis*, g: *R. micropylora*, h: *R. kerrii*, i: *R. arnoldii*, j: *R. rochussenii*, k: *R. schadenbergiana*, l: *R. cantleyi*, m: *R. hasseltii*. Drawn by Janis Atlee, from different photographs in archives W. Meijer (MO).

Taxonomy — Winkler [Planta 4 (1927) 1–97] suggested a subdivision based on the structure of ramenta, which appear to have great diagnostic value in tracing the possible phylogeny of species in this genus. Comparative research of the ribosomal RNA of surviving species can test this assumption.

Historical review — The first botanical explorer who found *Rafflesia* in Malesia was the prominent but ill-fated French surgeon-naturalist Louis Auguste Deschamps. He sailed from 1791 to 1794 during the great upheavals of the French revolution with the expedition of the 'La Recherche' in search of the lost research ship 'La Pérouse' (Van Steenis-Kruseman 1950; Van Steenis et al. 1954). In March 1794 the ships, after giving up the search, were in the harbour of Surabaya in East Java and the commander of the expedition refused to proceed in view of the situation in France. Deschamps and his companions let themselves be interned by the Dutch colonial authorities. Deschamps, who apparently showed great interest in the local language, people, flora and fauna was

invited by Governor Van Overstraten to make natural history studies all over Java for three years, making with the help of special assistants many notes, drawings and collections and even starting on a manuscript entitled 'Materials towards a Flora of Java'. That still marvelous island must during that time have been for him a botanical paradise. In 1798 he could return with his treasures to France but meanwhile the British were at war with the French and blockaded France from the sea. The ship on which Deschamps sailed was taken by the British and all the specimens and notes of Deschamps were confiscated.

Years later the manuscripts and some specimens turned up at a public sale at the Indian House in London and were bought by John Reeves, who donated them in 1861 to the British Museum (Natural History). The specimens were never seen again (Van Steenis-Kruseman 1950). It lasted until about 1954 when the manuscripts could be studied by C.A. Backer, Mrs and Prof. van Steenis, who to their surprise discovered that among these notes were sketches of buds and host plants of *Rafflesia*, most likely seen by Deschamps on Java, long before the well-known so-called first discovery of what somebody called that stupendous plant (Mabberley) by Arnold and Raffles in the southern part of Bengkulu (Benkoelen, Bencoolen) in Sumatra in 1818. There are suspicions by Mabberley and Van Steenis (unpubl. letters) that British botanists possibly knew that Deschamps had found a very strange plant and that there was a kind of secret competition going on to see who would first unravel further this wonder of nature. That might have been one of the reasons why the young and eager botanical explorer-surgeon-naturalist William Jack, replacing Arnold who died of malaria soon after he did his discovery, rushed at the instructions of Raffles a description of *Rafflesia* as *R. titan* Jack, already forwarded to Marsden by Raffles in April 1820, into print in August 1820 [see W.J. Hooker (1835) 135, 136] in an Appendix of his Malayan Miscellanies at the Missionary Press in Bengkulu. Actual publication of this Appendix was kept back while the Linnean Society took long to print the paper on *R. arnoldii* R.Br., read by Brown on 30 June 1820 at the meeting of this prestigious society. Whoever got the name first published it should be a British botanist. (See also page 35 under the Incompletely known species.) Rivalry between the British, French and Dutch was great at that time.

The supposition of Merrill (1952) that the names *R. arnoldii* and *R. titan* were based on the same types is wrong. Jack collected plenty of extra materials for Brown and himself after Raffles had forwarded letters and specimens to Sir Joseph Banks, who delegated the description to Brown (Mabberley 1985) and he also established for sure that the plant was a parasite on a kind of grapevine, later called the genus *Tetrastigma*. Soon after Jack had assured Robert Brown that his publication was only a kind of backup action he died of a lung disease and only a few copies of his Appendix had been sent by him to Wallich in Calcutta and to Brown, while the main shipment went into flames at sea not far from the harbour of Bengkulu with all of Raffles's belongings on his way back to England. Raffles managed to get ashore again and started a recollecting drive (Mabberley 1985). See also details on Jack in Hook. Comp. Bot. Mag. 1 (1835) 121–147. He was a marvelous very promising botanist like Arnold and later Kuhl and Van Hasselt who were less lucky than Deschamps to get out of malaria-infested Java alive.

Just a few years after Brown received letters from Jack about the fruits of *Rafflesia* and its host specificity another *Rafflesia* event unfolded in Java where since 1818 the very young and ambitious (only 22 years old in 1818) German-Dutch surgeon-naturalist C.L. Blume was stationed as inspector of vaccines and in 1822 as Director of the Buitenzorg (now Bogor) Botanical Garden. He used the fortune of his rich first wife to launch large expeditions in the wilds of Java, during one of which he found out about a large bud and some kind of flower in the Nusa Kambangan Peninsula along the southcoast of Java. He succeeded to find it, first did not recognize it as a flowering plant, but soon compared it with the excellent illustrations of the Bauer brothers who worked for Robert Brown. By the time he had returned to Holland the German plant collector A. Zippelius had found on Mount Salak near Bogor what appeared to be a second genus related to *Rafflesia*. Blume described his new *Rafflesia patma* and also the new genus and species which he named *Brugmansia zippelii*, unfortunately using a genus name already occupied in *Solanaceae*. In beauty and interesting flower biology this genus, now known as *Rhizanthes*, equals *Rafflesia* and the large plates and long descriptions in Flora Javae by Blume are very impressive although difficult to read in his elaborate Latin prose (Backer 1921).

Subsequently other discoveries were made: the very small *Rafflesia manillana* in Luzon (Teschemacher 1841); in 1850 a rather small novel *Rafflesia* species with a completely unarmed disk of the central column, collected by an unknown plant collector of the Bogor garden on the Gedeh-Pangerango outlayers near Cibodas and described by Teijsmann & Binnendijk (1850) as *R. rochussenii*. In 1884 *Rafflesia tuan-mudae* was found by O. Beccari in Sarawak. The Central Sumatra expedition of D.D. Veth in 1884 had the very distinct *R. hasseltii* as one of its main trophies. It was recently rediscovered by the French botanist-cartographer Yves Laumonier and by Harry Wiriadinata from Bogor.

Solms-Laubach (1891) commented on the two species known from the Philippines and he described in 1910 *R. cantleyi* from Malaya.

Meanwhile the few known localities of *Rafflesias* within easy access from Bogor had been mined out so much for all sorts of anatomical-morphological research and attempts to transplant the parasites wholesale attached to the hosts to the Bogor Botanic Garden, that the original localities became depleted.

Koorders (1918) described a number of new species from collections by Witkamp and others; Meijer (1984) added five and Mat Salleh & Latiff (1989) one. In 1992 *R. kerrii* was found back in the Malay Peninsula (Wong 1993).

References: Backer, C.A., Trop. Natuur 10 (1921) 124–127. — Koorders, S.H., Bot. Overzicht Rafflesiaceae Ned.-Indië (1918) 128 pp. — Mabberley, D.J., Jupiter Botanicus. Robert Brown of the British Museum (1985) 219–238. — Mat Salleh, K. & A. Latiff, Blumea 38 (1989) 111–116. — Meijer, W., Blumea 30 (1984) 209–215. — Solms-Laubach, H., Ann. Jard. Bot. Buitenzorg 9 (1891) 184–246, 28 pl. — Steenis, C.G.G.J. van, M.J. van Steenis-Kruseman & C.A. Backer, Bull. Brit. Mus. (Nat. Hist.) I, n. 2 (1954) 51–68, pl. 13. — Steenis-Kruseman, M.J. van, Cyclopaedia of collectors. Flora Malesiana I, 1 (1950). — Teijsmann, J.E. & S. Binnendijk, Nat. Tijds. Ned. Indië 1 (1850) 425–430. — Teschemacher, J.E., Boston J. Nat. Hist. 4 (1841) 63. — Wong, M., Nature Malays. 17 (1993) 124.

Ex situ cultivation — There are reports by Teijsmann (1850) and J.J. Smith (1929) about transplantations of *Tetrastigma* with *Rafflesia* from their natural sites to the Bogor Garden. In 1850 H.H. Loudon from Nusa Kambangan assisted with the transfer of *Rafflesia patma* [see a letter from Teijsmann to De Vriese, dated 23 July 1852 in De Vriese (1853)]. This plant flowered from 23 until 25 March 1850 and again the 6th of October. Docters van Leeuwen (1929) cited the same flowering dates and this proofs that in fact *R. patma* was not grown from seeds as he asserted. *Rafflesia rochussenii* was added to the garden collection from transplants after 29 July 1850 (Teijsmann & Binnendijk 1850). By 1856 *Rafflesia arnoldii* had been added to it (see Teijsmann 1856a; Teijsmann & Binnendijk 1866).

According to a short note in Botanische Zeitung of 15 May 1857 (p. 328), the Dutch newspaper Haarlemsche Courant of 7 April 1857 stated (translated): "*Rafflesia arnoldii* flowered on 9 February 1857 in the Botanic Garden of Buitenzorg, Java. This flower came from a plant which grew as the result of Teijsmann's attempts to inoculate a wild grape vine. The flower was immediately illustrated at the spot." Most likely this is the one figured by Miquel (1863).

As mentioned above, Teijsmann (1856a, b) reported in several papers about his inoculation experiment, also in a French version (Teijsmann 1858). Binnendijk, in a letter to Motley (Motley 1857), claimed that he in fact did the actual inoculation which took place in November 1854. The first buds were visible in August 1855 and as we saw the first flower appeared February 1857.

Seeds were said to have been taken from a fruit grown in the garden but it is rather obscure how the flower which produced that fruit was pollinated. Also the subsequent history as reported by Solms (1875) and Beccari (1875), suggesting that this plant was bisexual, self-pollinating or parthenocarpic is very confusing as already explained above. It shows that careful documentation and labelling in situ and good record keeping is absolutely needed in such experiments.

In 1866, there were three species of *Rafflesia* (*R. patma*, *R. arnoldii* and *R. rochussenii*) at the Bogor Garden according to the Garden Catalogue (Teijsmann & Binnendijk 1866). Docters van Leeuwen (1929) cited old mantri Noerkas as remembering a flower in 1879.

The situation in 1883/84 was described by Solms (1891). Beccari (1875) reported to have seen flowers of *R. patma* in Bogor when he visited the Gardens between 30 January and 2 February 1872.

Beccari saw *R. arnoldii* in the Bogor Garden in 1874 (Beccari 1875) and reported that the species flowered every year. Reports from Docters van Leeuwen can be projected back in time around 1889 and around 1898 according to J.J. Smith (1929). Raciborski made according to Smith new attempts to transplant *R. patma* from Nusa Kambangan. The last year *R. rochussenii* and *R. patma* flowered in Bogor was 1929 (Docters van Leeuwen 1929; J.J. Smith 1929). Since 1929 no further attempts were made by anybody connected with the garden since localities were depleted, partly due to over-collecting or totally destroyed by land cultivation or protected in tiny nature reserves (see also Brewer 1918).

Docters van Leeuwen wrote in a Dutch article (1929) that his horticulturist P. Dakkus repeated a seed inoculation experiment in August 1924 with seeds of *Rafflesia rochussenii* from a fruit supplied by Ader from Mt Garut. This was done in the Fern-Bromeliad Garden on stems of *Tetrastigma lanceolarium* (now *T. leucostaphylum*). In January of 1929, 4.5 years later, a flower appeared as a result of this. Dr. Frits Went made photographs of it.

Rafflesia rochussenii seems to be the only species of the genus that has ever flowered in a greenhouse in the temperate zone. De Vriese (1853) illustrated this species from a plant grown in the Leiden Botanical Garden. The infected host plant must have been transported in a wardian case by ship all the way from Java. I have not been able to find any special report about the actual flowering date in a local newspaper of that time nor a reference in Botanische Zeitung.

References: Beccari, O., Nuovo Giorn. Bot. Ital. 7 (1875) 70–75. — Brewer, F.W.J., Meded. Natuurmon. Ned.-Indië nr. 2 (1918) 19–21. — Docters van Leeuwen, W.J., Trop. Natuur 18 (1929) 43–45. — Miquel, F.A.W., Choix des plantes rares ou nouvelles cultivées et dessinées dans le Jardin Botanique de Buitenzorg (1863) pl. 1. — Motley, J., Extract from a letter. Hook. J. Bot. & Kew Gard. Misc. 9 (1857) 148–153. — Smith, J.J., Trop. Natuur 18 (1929) 156. — Solms-Laubach, H., Abh. Naturf. Ges. Halle 13, 3 (1875) 40 pp., t. 24–27; Ann. Jard. Bot. Buitenzorg 9 (1891) 184–246. — Teijsmann, J.E., Nat. Tijds. Ned. Indië 1 (1850) 431–440; ibid. 12 (1856a) 279–281; Hook. J. Bot. & Kew Gard. Misc. 8 (1856b) 371–374; Ann. Hortic. Bot., Fl. Jard. Roy. Pays-Bas (1858) 27–30. — Teijsmann, J.E. & S. Binnendijk, Nat. Tijds. Ned. Indië 1 (1850) 425–430; Cat. Plant. Hort. Bot. Bogor. (1866) 15. — Vriese, W.H. de, Mémoire sur R. rochussenii et patma (1853) 9 pp., 2 pl.

KEY TO THE SPECIES AND VARIETIES

1a. Ramenta short, more or less pustulate, only a few millimetres long, in some cases clavate 2
b. Ramenta more than 2.5 mm long 4
2a. Flowers 15–20 cm in diam. Opening of diaphragm (orifice) relatively wide, leaving the lower inner side of the flower tube exposed to view from above. Anthers c. 15 ..... **7. R. manillana**
b. Flowers at least 25 cm in diam. Orifice of diaphragm too small to expose the inner side of the flower tube. Anthers 20–40 3
3a. Flowers (15–)30–60 cm in diam. Rim of disk steeply raised. Anthers (25–)32–40. Ramenta very short knobs ..... **9. R. patma**
b. Flowers 26–30 cm diam. Disk rim only slightly raised. Anthers about 20 ..... See *R. borneensis*, under Incompletely known species, *p. 34*
4a. Perigone lobes and diaphragm in general red or orange throughout, including the warts. Diameter of flowers on average 20 cm (15–30). Ramenta slender and swollen at apex 5
b. Perigone lobes with white warty blots, or disk with many processes, or flowers larger than 30 cm diam. (*R. micropylora*) 6
5a. Disk of flowers totally smooth or with up to 8 processes, rim not raised. Anthers 15–20 ..... **11. R. rochussenii**
b. Disk with c. 25 processes, rim raised. Anthers 20 ..... **13. R. tengku-adlinii**

6a. Orifice of diaphragm angular or slightly lobed, very small compared to the size of the flower, 3–9 cm in diam., too small to be able to count the c. 15 processes. Ramenta often branched and apices of branches globular, swollen. Flowers 30–60 cm diam. Warts on perigone lobes reddish ..... **8. R. micropylora**
b. Diaphragm opening relatively larger 7
7a. Apices of the ramenta either more or less distinctly swollen or crateriform ... 8
b. Apices of the ramenta not distinctly swollen 10
8a. White warts across the base of the perigone lobes very large, 4 or 5 only. Ramenta slender, apices swollen. Anthers c. 20. Diaphragm with only one basal ring of dark-brown warts ..... **4. R. hasseltii**
b. White warts across the base of the perigone lobes more than 5. Diaphragm with several concentric rings of warts..... 9
9a. White warts across the base of the perigone lobes 10–12. Some ramenta with swollen, others with crateriform apices. Anthers c. 30 ..... **3. R. gadutensis**
b. White warts across the base of the perigone lobes 7–9. Ramenta slender, all with swollen apices. Anthers 20–25 ..... **2. R. cantleyi**
10a. White warts in tangential direction about halfway along the perigone lobes relatively covering less space than the red parts, c. 8 in number ..... See *R. tuan-mudae*, under Incompletely known species *(p. 36)*
b. White warts on perigone lobes more numerous 11
11a. Flowers c. 70 cm in diam. White warts on the perigone lobes very small, covering far less space than the red-coloured part. Anthers (20?–)24–30 ..... **6. R. kerrii**
b. White warts on the perigone lobes covering more space than the red-coloured part 12
12a. White warts across the base of the perigone lobes 5 or 6(–10) 13
b. White warts across the base of the perigone lobes more than 10..... 14
13a. Flowers up to 80 cm diam. Lower face of the diaphragm with ramenta. Anthers 26–38 ..... **12. R. schadenbergiana**
b. Flowers (16–)25–37.5 cm diam. Lower face of diaphragm without ramenta. Anthers c. 20 ..... **10. R. pricei**
14a. Larger white blots on perigone lobes interspaced with numerous small ones. Circular blots on diaphragm contrasting, isolated and with broad dark-brown margin ..... **5. R. keithii**
b. Larger white blots on perigone lobes not or very sparsely interspaced with smaller ones. Circular white blots on the diaphragm little contrasting with their surrounding tissues, often more or less connected in a network of dark reddish bands and with only a thin dark redbrown margin 15
15a. Ramenta covering the inner side of the flower tube from the rim of the diaphragm downwards to the outer annulus ..... **1a. R. arnoldii** var. **arnoldii**
b. Ramenta missing in a zone above the outer annulus at the base of the column ... . **1b. R. arnoldii** var. **atjehensis**

1. Rafflesia arnoldii R.Br.

Rafflesia arnoldii R.Br., Trans. Linn. Soc. 13 (1821) 201; 19 (1845) 221, t. 22–26; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 237, t. 27, 28; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 31, pl. 1, 2, 3; Coomans de Ruiter, Trop. Natuur 22 (1933) 165; 188 (as *R. tuan-mudae*); Meijer, Nat. Geogr. 168 (1984) 136. — Type: *Raffles & Arnold s.n.* (K).

a. var. arnoldii

Mature *buds* up to 30 cm diam. *Flowers* (55–)70–100 cm in diam. *Perigone lobes* with up to c. 15 white warts in radial and lateral direction, only occasionally interspersed with smaller white warts, the white warts occupying slightly more space than the reddish brown background. Processes on the disk (20–)35–40(–50). *Diaphragm* with an opening about 2/3 of the total diaphragm diameter, raised rather high at the end of flowering phase, upper face light reddish pink with c. 40 radial series of 4 or 5 white circular warts which are only a few mm in diameter, lower face just below the rim with 3 or 4 series of white rounded blots. *Ramenta* up to 10 mm long when mature, all over the inner side of the flower tube, simple or forked and when fresh with papillose fluffy apices, never crateriform swollen like in *R. gadutensis*. *Male flowers* with 36–40 anthers.

Distribution — *Malesia:* Sumatra (Aceh, W Sumatra, Bengkulu, Lampong), Borneo (W Sarawak, W Kalimantan).

Habitat — Primary and disturbed lower montane forests, up to c. 1000 m altitude.

Ecology — Host plant most commonly *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb. [= *T. lanceolarium* (Roxb.) Planch.].

Notes — 1. See also under Incompletely known species, *Rafflesia tuan-mudae* Becc., p. 36.

2. A plant of this species flowered on 9 February 1857 in the Bogor Botanical Garden. See paragraph on ex situ cultivation, p. 20.

b. var. atjehensis (Koord.) Meijer

Rafflesia arnoldii R.Br. var. *atjehensis* (Koord.) Meijer, comb. et stat. nov. — *Rafflesia atjehensis* Koord., Bot. Overz. Raffles. Ned.-Indië, Nieuwe Addenda (1918) 11; Bull. Jard. Bot. Buitenzorg 3 (1918) 77, 3 pl. — Type: *Koorders 44060* (BO).

This variety differs only in the almost glabrous, 2 cm wide zone at the base of the perigone tube, with only scattered, very short (3–6 mm long) ramenta.

Distribution — So far only known from the type locality Aceh, Locop. Possibly also near Bohorok near the boundary of the Leuser National Park.

Habitat — Lowland Dipterocarp forest.

2. Rafflesia cantleyi Solms-Laubach

Rafflesia cantleyi Solms-Laubach, Ann. Jard. Bot. Buitenzorg, Suppl. 3 (1910) 1. — Type: *Cantley s.n.*, received at Kew in 1887, fragments given to Solms in 1901, seen by the author in STR.

Rafflesia hasseltii auct. non Suringar: Meijer, Mal. Naturalist 36 (1983) 21, 2 col. photos, map; Wong, Nature Malays. 15 (1990) 56–59, col. photos.

Flowers c. 30–55 cm across, in all respects very much like *R. hasseltii* but *perigone lobes* with about 6–8 big whitish warts in radial and lateral direction and up to 10 in the basal rows, sometimes these blots more or less confluent in bizarre wavy edged configurations. *Diaphragm* opening rounded or angular, almost half as wide as the total diameter, 4–8 cm broad upper face light pinkish or whitish with about 25 radial series of 3 or 4 dark red circled dots; lower face above the insertion with 3 concentric series of stalked toadstool-like ramenta, with 5 mm long stalks and capped by 5–8 mm wide disks, towards the rim 5 concentric series of oval white blots, 12–15 mm wide and 8–10 mm in radial direction. *Ramenta* covering the inner face of the *flower tube* 10–12 mm long, partly branched, with swollen apices, papillose grainy, lower down shorter, c. 2 mm long. *Male flowers* with 20–25 anthers.

Distribution — *Malesia:* Malaya (Perak, Kelantan, Pahang, Tioman I., Kedah), see map in Meijer, l.c. 1983, updated (in ms) by Matthew Wong. See also Meijer & Wong, Mal. Naturalist 47 (1993) 10–11.

Habitat — Lowland Dipterocarp forest and secondary forest.

Notes — 1. This species was up to 1984 considered by the author to be identical with *R. hasseltii* Suringar, following identification by Ridley and others.

2. See also note 2 under *R. hasseltii*.

3. Rafflesia gadutensis Meijer

Rafflesia gadutensis Meijer, Blumea 30 (1984) 211; Weevers in Koningsberger (ed.), Leerb. Alg. Plantk. 2 (1942) f. 186 (as *R. arnoldii*); Richards, Trop. Rain Forest, ed. 2 (1996) 155: f. 6.23; Meijer, Palmengarten 60/2 (1997, '1996') 38–41. — Type: *Meijer 17003* (BO holo; MO), W Sumatra.
Rafflesia spec.: Schaefer, Trop. Natuur (1940) 21–23;

Flowers 40–46 cm diam. *Perigone lobes* with 10–12 whitish-pinkish blots along the median and along the base, largest blots 2 by 1 cm, few small blots in between, some of the larger sometimes merged and up to 5 cm broad. *Diaphragm* opening about 2/3 of the total width, pinkish red with about 30 radial rows of circular light pinkish red margined warts, lower face of diaphragm with 5 concentric rings of white blots close to the rim, the two rings of warts closest to the perigone tube with flat or somewhat crateriform oval fringed apex, c. 9 by 8 mm across, the tops supported by 1–2(–6) mm long stalks, making them look like minuscule toadstools. *Perigone tube* c. 8 cm deep, covered at the inside with rather fugaceous ramenta which are 6–8(–9) mm long and have swollen heads 1 mm long and 2–3 mm wide, sometimes crateriform at apex, stalks c. 1 mm across, a few branched or lobed ones near the diaphragm. Between the ramenta on the inner side of the perigone tube some scattered toadstool-like protuberances close to the inside of the diaphragm, but with only 1–2 mm long stalks. *Male flowers* with c. 30 anthers. — **Plate 1.**

Distribution — *Malesia:* W Sumatra (Westcoast, Ophir District, Padang–Bukittinggi; Bengkulu, Kayu Tanam, Padang–Solok, Ulu Gadut).

Habitat — Primary and secondary lower montane forest, around 350–600 m altitude.

Notes — 1. First seen by Korthals around 1834 and illustrated for him but unpublished; also copies made for Solms-Laubach. Also found near the gold and silver mine Simau, Bengkulu, and photographed there around 1934 by K. Schaefer [see Schaefer, Trop. Natuur 29 (1940) 21–23].

2. Beccari collected the species in August 1878 near Ayer Mancior, the waterfall in the Anei Canyon between Padang and Bukit Tinggi, at about 360 m altitude near Kayu Tanam, West Sumatra. He and Solms-Laubach misidentified this species as *Rafflesia arnoldii*.

4. Rafflesia hasseltii Suringar

Rafflesia hasseltii Suringar, Acta Soc. Reg. Sc. Neerl. 25 Oct. 1879 (1880?) [4–5]; Assoc. Avanc. Sciences, Congr. Alger (1881) 621–626, pl. 11, 12; in Veth, Midden-Sumatra (1884) 13, t. 1, 2; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 23; in Engl., Pflanzenr. 5 (1901) 9, f. 1; Ann. Jard. Bot. Buitenzorg 3, Suppl. pt 1 (1910) 1–4, pl. 1–6; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 76–81, pl. 12; Theunissen, Trop. Natuur 13 (1924) 150–152, 2 f.; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 264; Meijer, Grasduinen 5 (1991) 65, photo. — Type: *Suringar* (L).

Flowers c. 38–50 cm diam. *Perigone lobes* c. 11.5–13 cm long and 15–17 cm wide, with about 5 large pustules across, these ranging from 5 by 3 to 10 by 1 cm. *Perigone tube* c. 18–20 cm wide, neck of column 3 cm. Processes 15–24, coloured like the disk, light yellowish, but dark brown at the apex and not flattened as in some other species. *Diaphragm* opening about half as wide as apex of flower tube, pale whitish or yellowish with a dark brown zone near the rim and a basal ring of rounded or oblong dark brown warts. Upper zone of the flower tube near attachment of the diaphragm with 4 rings of toadstool-like compound *ramenta*, grading into white blots at the lower face of the diaphragm. Numerous bristles on lower face of the corona (= crest of the disk) and all along the column. Ramenta linear, with swollen apices. *Male flowers* with 20 anthers.

Distribution — *Malesia:* Sumatra (W Sumatra, Riau, Jambi), Peninsular Malaysia.

Habitat — Primary and secondary lower montane forest, around 400–600 m altitude.

Notes — 1. Of the six localities known four were located during the last 10 years.

2. This species is closely related to *Rafflesia cantleyi* and seems to hybridize with it in the Malay Peninsula.

3. The description was composed from the original one and from a few fragments of the type in L and some photographs. Most records come from pictures.

5. Rafflesia keithii Meijer

Rafflesia keithii Meijer, Blumea 30 (1984) 211; Salleh & Latiff, Blumea 34 (1989) 113. — Type: *Madani s.n.* (SAN holo, in spirit), Sabah, Sungai Melaut.

Rafflesia spec.: Corner in Luping et al., Kinabalu, summit of Borneo. Sabah Soc. Monogr. (1978) 136, 168, t. 154, photos.

Mature *buds* up to 25 cm diam. *Flowers* on average c. 80(–94) cm in diameter (few records). *Perigone lobes* with rather dense numerous white warts, small ones interspers-

ed with larger ones, the latter about 10–12 across the greatest breadth of the lobes. *Diaphragm* with 5 concentric rings of white warts in about 40 radial rows, each surrounded by a dark red brown margin, lower face of diaphragm with 5 or 6 rings of white blots, those of the ring closest to the opening for a large part confluent, towards the transition into the flower tube not with ramentae formed like white-headed toadstools (stalked disks), but uniformly with the same type of long ramentae as those on the inner side of the flower tube. *Perigone tube* densely covered with ramenta inside, the ramenta 5–6 mm long near the diaphragm and often fascicled (in bundles), only a few branched. Disk 11–13.5 cm in diam. Processes 38–42(–46), flattened. Annulus interior in a bud of 22 cm diam., 2 mm wide, annulus exterior flat, 5 mm wide and grooved. *Male flowers* with about 40 anthers and with dense bristles on the lower face of the crest of the disk and around the anther cavities. *Female flowers* with a swollen ring along the lower rim of the crest of the disk, c. 3 mm high and broad. — **Plate 2.**

Distribution — *Malesia:* Borneo (Sabah, most likely also in E Kalimantan, see *R. witkampii* under Incompletely known species, p. 36).

Habitat — Upper Dipterocarp forest with *Parashorea malaanonan*, around 500–600 m altitude.

Ecology — Host plant *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb., very possibly also *T. diepenhorstii* Miq. (= *T. trifoliolatum* Merr.) but proof only from the former with a host plant with very low branches.

Notes — 1. At first sight this taxon comes close to *R. arnoldii* as defined in this revision. However, close study of the ramenta reveals that the single, toadstool-shaped ones that are typical for *arnoldii* are missing in *keithii* (and in *pricei*, possibly the nearest relative of *keithii*). This view is supported by the occurrence of a hybrid at the Mamut copper mine *Rafflesia* sanctuary in Sabah (Jamili Nais, oral comm.).

2. A main problem is still the lack of good documentation and sharp colour photographs of *Rafflesia* specimens with mature flowers from E Kalimantan.

6. **Rafflesia kerrii** Meijer

Rafflesia kerrii Meijer, Blumea 30 (1984) 212; Meijer & Elliott, Nat. Hist. Bull. Siam Soc. 38 (1990) 117–133. — Type: *Kerr 16980* (K holo; BM), Phuket.

Flowers up to 70 cm diam. *Perigone lobes* up to c. 20 cm long and 24 cm wide, with scattered rather numerous warts, with 3–4 mm space between them, the warts smallest relative to the red background of any species known. *Perigone tube* with ramenta which are mostly unbranched and only slightly swollen at apex, those near the diaphragm c. 10 mm long, those near the base of the tube 5 mm. *Diaphragm* only slightly lighter red than the perigone lobes, about 30 cm in diameter with a central opening about 20 cm across; upper face with about 3 to 4 concentric rings of circular whitish, dark red ringed spots, in about 30 radial lines; lower face with 7 concentric rings of white blots, which are up to 7 mm across. Central part of disk with 32–40 flattened processes, 2–2.5 cm long. *Male flowers* with 25–30 anthers.

Distribution — Peninsular Thailand; *Malesia:* Peninsular Malaysia (Kelantan: Bukit Tepoh; Kelantan-Perak border: Mt Chamag; Perak: Bintang Range).

Habitat — Lowland and hill Dipterocarp forests, 500–1000 m altitude.

7. **Rafflesia manillana** Teschemacher

Rafflesia manillana Teschemacher, Boston J. Nat. Hist. 4 (1841) 63, t. 6; Ann. Mag. Nat. Hist. 9 (1842) 381; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 241, t. 26, f. 7–10; W.H. Br., Philipp. J. Sc., Bot. 7 (1912) 209, t. 12, 21; Merr., Spec. Blanc. (1918) 135; Enum. Philipp. Flow. Pl. 2 (1923) 120; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 264; Pancho, Vasc. Fl. Mt Makiling (1983) 312, f. 98. — Type: *Navarro* specimen from Leyte (A, lost).

Rafflesia philippensis Blanco, Fl. Filip., ed. 2 (1845) 565. — Type: *Navarro* specimen from Laguna, Luzon, now lost.

Rafflesia lagascae Blanco, Fl. Filip., ed. 3, 3 (1879) 231; most likely a nomen nudum.

Rafflesia cumingii R.Br., Trans. Linn. Soc. 19 (1845) 243. — Type: *Cuming* collection (BM), most likely from the same site on Leyte as the *Navarro* collection seen by Teschemacher.

Flower buds up to 8 cm across, cupule 2.5–3 cm high, 4–6 cm wide, bud scales up to 5.5–7 cm long. *Flowers* 15–20 cm wide and 7–9 cm high when expanded. *Perigone lobes* light reddish brown, 4–6 cm long and 5–7 cm wide, white warts a mixture of larger circular with oval ones, about 10–12 along a transverse line halfway the lobes, mixed with numerous white dots. *Diaphragm* c. 1–1.4 cm broad, c. 7 cm in diameter, strongly curved inwards along the opening, which is about 5/6th as wide as the apex of the perigone tube; upper face rather densely randomly covered with oblongish white warts. *Disk* of column c. 2 cm above the base of the perianth tube, 3.2–4.5 cm in diameter including the rim, exposed while the flower is opened; rim of disk with a 3–5 mm high raised part. *Processes* about 14–20(–30), sometimes almost missing in the centre of the disk, 3.5–5.5 mm long, apex cylindric, with bushy cilia. Neck of *column* 1.3–1.8 cm diameter, narrower in male flowers. One prominent annulus, 3 mm broad, 30–38 mm diameter around the base of the column. *Perigone tube* c. 2.5 cm deep, 5 cm wide; ramenta at the inner side in about 12 rows, little stalked outgrowths, 0.5–1 mm high, multilobed at apex, virtually absent near the base of the perianth tube, close to the annulus; in a 1 cm wide zone below the diaphragm with short, warty lobed, whitish, 2–3 mm wide warts. *Male flowers* with 10–15 anthers, relatively large for such small flowers, not hidden in a sulcus as in the larger-flowered species, but attached rather close to the lower margin of the disk; corresponding with each anther in the central column a deep groove which runs down below the anther to the column base. *Female flowers* with ovary 2.5 cm wide at apex, 1.0 cm high, above the annulus without grooves or with very faint ones, less room under the corona (overhang) of the disk than in male flowers, on its lower side a papillose stigmatic zone.

Distribution — *Malesia:* Philippines (Luzon, Samar, Leyte). Most of these records are old history. The species is now rare and endangered.

Habitat — Lowland and hill forests, up to about 1000 m altitude.

Note — This is the smallest known *Rafflesia*, with flowers only about 15–20 cm in diameter, a very narrow diaphragm, the whitish lobed ramenta only up to 1 mm tall and male flowers only with 10–15 anthers.

Plate 1. *Rafflesia gadutensis* Meijer. Sumatra, Ulu Gadut near Padang. Photo W. Meijer, 1983.

Plate 2. *Rafflesia keithii* Meijer. Sabah, Sabah, Mt Kinabalu. Photo Jamili Nais, 1990, donated 1994.

Plate 3. *Rafflesia micropylora* Meijer. Sumatra, Mt Leuser National Park. Photo A. Rijksen.

Plate 4. *Rafflesia pricei* Meijer. Sabah, Tambunan. Photo Julius Kulip, 1989, donated 1992.

8. Rafflesia micropylora Meijer

Rafflesia micropylora Meijer, Blumea 30 (1984) 213. — Type: *Koorders 44211* (*Badings s.n.*) (BO holo), Lokop.

Rafflesia cf. *atjehense* auct. non Koorders: W.J. de Wilde, WOTRO-Jaarboek (1972) 38, fig.

Rafflesia spec. 3 and *spec. 4*: Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 109, 111. See note 2.

Flowers 30–60 cm diameter, no data available on size of buds. *Perigone lobes* dark orange-red all over, 16–18 cm long, warts light pinkish, little contrasting with their surroundings, about 10 across at the base, with many smaller warts in between. *Diaphragm* darker red than the perigone lobes, c. 20–25 cm diameter, upper surface with 3–5 concentric circles of circular reddish warts with darker red margins, weakly contrasting, in about 40 radial lines; lower side of diaphragm with about 3(–5?) concentric circles of flat circular knobs, c. 10 mm in diameter, on 5 mm high stalks, grading into the ramenta towards the upper rim of the perigone tube; opening small, c. 3–9 cm wide, sexangular or heptangular, sometimes weakly lobed. *Column* 5–6 cm high, c. 7–8 cm in diameter at the neck. *Disk* 13–14 cm diameter, with about 15 processes. *Ramenta* branched, with swollen apices, c. 12 mm long, those towards the base of the perigone tube only 5-7 mm long and unbranched. *Male flowers* with 40 anthers. — **Fig. 6; Plate 3.**

Distribution — *Malesia:* Sumatra (Aceh). Protected inside the Leuser National Park.

Habitat — In lower montane forests around 300–500 m altitude.

Ecology — Host plant *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb., and possibly other species.

Notes — 1. The medium- to large-sized flowers, the small opening of the diaphragm and the richly branched ramenta with swollen apices, make this species easy to recognize.

2. The red-coloured diaphragm, together with the size and the small hole as illustrated in Koorders (l.c.: plate 15, fig. G), make identification of the two numbered species now possible.

9. Rafflesia patma Blume

Rafflesia patma Blume, Flora 8 (1825) 609; Flora Javae 1 (1828) 8, t. 1–3; De Vriese, Mém. sur Rafflesia Rochussenii et Patma (1853); Illustr. Rafflesia (1854) t. 5, 6; Rodigas, Fl. Serres 15 (1862–65) 13, t. 1505–1508; Nagelvoort, Nat. Tijds. Ned. Indië 35, VII, 5 (1875) 171–180; Haak, Weekbl. Pharm. 3 (1885) 19 pp., 2 pl.; Observ. Rafflesia patma (1889) 4 pl.; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 238–239, pl. 16, f. 11–16; in Engl., Pflanzenr. 5 (1901) 9, f. 2, 5; Koord., Exk. Fl. Java 2 (1912) 179; Warb., Pflanzenwelt 1 (1913) t. 31, f. D1–5; Hochr., Le Globe 57 (1918) 27–36, photo; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 50–61, pl. 6; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 263; Backer & Bakh. f., Fl. Java 1 (1963) 165. — Type: *Blume* (L), Nusa Kambangan.

Rafflesia zollingeriana Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 67, pl. 10, 11; Backer & Bakh. f., Fl. Java 1 (1963) 165; Ervizal, Masters thesis (unpubl.) Agric. College Bogor (1989). — Type: *Koorders 40312* (BO), Java, Puger.

Flower buds prior to expansion up to 21 cm in diameter. Open flowers (30–)37–52 (–60) cm in diameter (in flowers described as *R. zollingeriana* sizes of 20–25 cm re-

ported). *Perigone lobes* flesh-coloured, brown-ocre or carmine red, c. 13–14(–19) cm long and 10–14 cm wide, on the upper face with numerous whitish warts, up to about 25 at the largest breadth, surrounded by much smaller white warts, then same pattern as in *R. keithii*. *Diaphragm* a 5–7 cm wide ring; opening in the centre 5–9 cm across; upper surface strongly pitted, glaucous or with clear circular whitish blots; lower face with 2 series of white oblong-angular blots, two to three times as long tangentially than radially, covered with ramenta or in some cases the region (2–)3–3.5 cm from the margin of the opening and the zone close to the perianth tube devoid of ramenta. *Disk* carmine red, upper face 6–6.5 cm from the bottom of the cupule, (7–)9–13.5 cm in diameter, central part with (24–)37–44(–54) processes 2–3 cm long and 5–8 mm at base, conical or somewhat flattened; corona of the column-disk about 2–2.5 cm high and 1.5 cm wide in radial direction, rim in some cases crenulate, papillose and fimbriate, directed sideways under an angle of about 45°. *Ramenta* reduced to very short (up to 1 mm long) tubercles, some branched. *Male flowers* with about 25–32(–38 in S Sumatra) anthers, 4–6 mm long and across, attached at the inner margin of the corona in a more or less horizontal position, anther cavities 10–15 mm long and 8 mm broad, weakly or not divided by two ridges, partitions between the anther holes provided with cilia. *Female flowers* with a 2–4 mm broad, slightly papillose stigmatic zone divided by a groove; rudimentary anthers c. 1–1.5 mm, in very shallow, broadly triangular cavities. Gully at the neck of the column (sometimes referred to as Sulcus coronalis disci) about 8–9.5 cm in diameter, c. 17 mm from the rim of the corona. Annulus interior 4–6 mm broad, well defined and sharply elevated (2–3 mm high), or only slightly raised, about 8–9.5 cm in diameter. Sulcus inter annuli 3–5 mm wide. Annulus exterior 3–10 mm wide average and c. 1 mm thick, rather weakly developed, wrinkled like a rolled-up blanket which is curved into a circle. *Fruit* with cupule 11 cm in diameter, 7–8 cm high, diameter in upper part 7.5 cm, ovarial part 1–2.5 cm high and 5–10 cm wide, side of column with about 40 grooves. Ripe *seeds* 0.8–0.9 mm long, 0.4 mm thick, light-brown to dark-brown.

Distribution — *Malesia:* S Sumatra (Lampong, now extinct?; C and E Java (close to extinction), possibly formerly also in Bali.

Habitat — Most localities are along the south coast of Java in remnants of forest below 400 m altitude.

Ecology — Host species most commonly *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb., but possibly also *T. glabratum* (Blume) Planch.

Notes — 1. A medium-sized *Rafflesia*, at first sight much like *R. arnoldii* but the lower side of the diaphragm often covered with ramenta. Warts on the perigone lobes are a mixture of larger and smaller ones, more or less as in *R. keithii* from Borneo. The flower tube is more or less covered with very short knob-like ramenta, not more than one mm long, in some forms partly missing.

2. A form from East Java, with smaller flowers and ramenta almost absent in the lower part of the flower tube, was described by Koorders as *R. zollingeriana*. Ervizal (1989) found there in 1989 still viable populations.

10. Rafflesia pricei Meijer

Rafflesia pricei Meijer, Blumea 30 (1984) 214; Beaman & J.H. Adam, Sabah Soc. J. 7 (1984) 208–212; Beaman c.s., Amer. J. Bot. 75 (1988) 1148–1162; Mat Salleh, Rafflesia magnificent flower of Sabah (1991), several pl.; Meijer, Grasduinen 5 (1991) 63. — Type: *Price s.n.* (K holo), Mt Kinabalu.

Rafflesia schadenbergiana auct. non Goeppert: Meijer, Kosmos 5 (1982) 60, fig.

Rafflesia tuan-mudae auct. non Becc.: Anderson, Bioscience 26, 10 (1976) cover plate; Weber, Sabah Soc. J. 3 (1967) 11, t. 1, 2; Yong, Magnificent Pl. (1981) 2, fig.; Bailes, Kew Mag. 2 (1985) 275, fig.; Jacobs, Trop. Rainforest (1988) 241.

Rafflesia spec.: Dorst, Avant que nature meurt (1965) 153, t. 10; Price, Proc. Cotteswold Nat. Field Club 35 (1968) 93; Morley, Wild Flowers of the World (1970) t. 117C; McKinnon, Borneo (1975) 22, fig.; Bellamy, Botanic Man (1978) 60, fig.; Ayensu, Jungles (1980) 49; Masni, Bt Jubil, Kajian Ekologi dan taksonomi Rafflesia di Sabah khususnya di Tambunan, Thesis Univ. Kebangsaan Malaysia (1984); Beaman & J.H. Adam, Sabah Soc. J. 7 (1984) 208.

Mature *buds* c. 15–20 cm in diameter. *Flowers* (16–)25–30(–45?) cm across. *Perigone lobes* 7–10 cm long and 6.5–14(–19) cm wide, with 10–15 warts at base, many of those wider in the tangential than in the radial direction, some confluent. *Perigone tube* c. 14 cm wide. Column 3–4 cm high, c. 4–5(–9.5?) cm in diameter at the neck. Disk 8.5–9 cm diameter, with 20–40 flattened processes which are about 1–3.5 cm long and up to 1–1.5 cm in diameter. *Diaphragm* (7–)12–13(–17) cm diameter, opening c. 4.5–8.5 cm in diameter, slightly angular and with a white rim surrounded by a dark brown margin; upper face of diaphragm with four concentric rings of warts, those in the third ring from the centre sometimes linear, in the second ring more circular and especially in these two rings surrounded by dark brown margins; lower face of diaphragm with 4 or 5 concentric rings of laterally stretched white bands, without ramenta. *Ramenta* near the diaphragm in fascicled groups, slender, only slightly widened at apex, 2–6 mm long near the insertion of the perigone lobes and 6–7 mm at the base of the tube. *Male flowers* with 20 anthers. — **Plate 4.**

Distribution — *Malesia:* Borneo (Sabah, Sarawak, Brunei, also Kalimantan?). Apparently most populations are on Mt Kinabalu and the Crocker Range and Schwaner Range in Sarawak.

Habitat — Upper Dipterocarp forests with *Shorea platyclados* and lower montane forests, about 400–1300 m altitude.

Ecology — Host species *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb.

Notes — 1. This species apparently is now also known from Sarawak (Serian area) and it is possible that a recent discovery of *Rafflesia* by Danna J. Leaman (University of Ottawa) in the Upper Kajan near Long Ampin (East Kalimantan) also belongs to this species.

2. Probably the first collection was made by Joseph and Mary Clemens (nr *28512*), on 17 March 1932, near Dallas on Mt Kinabalu. However, we are not quite sure because the specimen does not show the pattern of the warts on the perigone lobes and the size of the flower is almost too large for this species, though the label records "diameter 13–18 inches" (= 32.5–45 cm). Meijer (in Dorst 1965) was the first to publish a photograph of this species on Mt Kinabalu.

11. Rafflesia rochussenii Teijsm. & Binn.

Rafflesia rochussenii Teijsm. & Binn., Nat. Tijds. Ned. Indië 1 (1850) 425–430, t. 1, 2; 2 (1851) 651–655; De Vriese, Mém. sur Rafflesia Rochussenii et Patma (1853) 4; Illustr. R. Rochussenii (1854) t. 1–3; Solms-Laubach in Engl., Pflanzenr. 5 (1901) 10, f. 6, 7; Ann. Jard. Bot. Buitenzorg, Suppl. 2 (1898) 3–12, t. 1; Ernst & Schmid in Ann. Jard. Bot Buitenzorg II, 12 (1913) 1–58; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 82, incl. var. *subaculeata* Koord., l.c. 87; Steenis, Trop. Natuur 30 (1941) 179–181. — Type of species and variety: from W Java, lost.

Mature *flower buds* just before opening c. 10–13 cm in diameter. Flowers (15–) 17–20(–30) cm in diam., c. 12 cm high. *Perigone lobes* c. 6.5–8(–9) cm long and 8–9(–11) cm wide, 7–10 cm at insertion. *Diaphragm* c. 11 cm in diam., 2.5–4 cm broad, lower surface covered with short (1–2 mm long) ramenta. *Disk* c. 5.5–6 cm above the base of the cupule, (6–)7–9 cm in diameter, ivory white when fresh, flat or slightly raised in the centre, rim sharp, not raised, centre without processes or with only 1–8 ('var. *subaculeata*'). Sulcus below the disk c. 5 cm in diam. Neck of column 4.5–5.5 cm in diam. *Perigone tube* 12 cm wide in the middle between annulus interior and diaphragm; annulus interior 6.5–7 cm in diam., rather sharp, 2–4 mm thick; annulus exterior a flat 6–8 mm broad zone without ramenta. *Ramenta* long stalked subdiscoid knobs, c. 10 mm long near the base of the perigone tube. *Male flowers* with 15–20 anthers. *Female flowers* with stigmatic ring distinctly narrowed. *Fruits* c. 8.5 cm wide and 7 cm high, ovary 6 cm wide and 3 cm high, disk decayed, cupula (5–)7–8 cm diam., 1.5–2 cm high.

Distribution — *Malesia:* W Java, N Sumatra (Mt Leuser and further south in Tapanuli). In 1989 and 1990 two sites were rediscovered on Mt Salak, Java, and one around 1995 on Mt Gede, Java (collected by Arindansyah, oral comm. by H. Wiriadinata). The species probably still occurred in Berastagi, Sumatra, in 1980. The site was, however, logged and destroyed in 1981.

Habitat — Lower montane forests up to about 1500 m altitude.

Notes — 1. The most distinctive character is the disk of the column with the rim only slightly raised and the surface bald or only with a few processes, never more than eight. The ramenta are slender and in general have knob-like apices.

2. Cultivated in the Leiden Botanical Garden in 1851 from dug-up plants (see paragraph on ex situ cultivation, p. 20) and illustrated from damaged flowers by De Vriese in 1853 and 1854.

12. Rafflesia schadenbergiana Göpp.

Rafflesia schadenbergiana Göpp. in Hieron., Bull. Internat. Bot. Horticult. St. Petersb. ('1884', 1885) 35–36, 1 pl.; Gartenflora 34 (1885) 3–7, pl. 1177; Ueber Rafflesia schadenbergiana Goepp., Ein Beitrag zur Kenntnis der Cytinaceen (1885) 1–10, t. 1, 2; Solms-Laubach, Bot. Zeitung (1885) 507; Ann. Jard. Bot. Buitenzorg 9 (1891) 189. — Type: *Hieronymus s.n.* (K, WRSL iso?).

Flower buds prior to expansion 16–20 cm in diameter, cupule 10–14 cm in diameter, bracts up to 17–18 cm long, 12–13 cm wide. Open *flower* about 80 cm diameter. Ramenta on the inside of the *flower tube* 7–10 mm long, filiform, somewhat thickened at apex, or branched, partly in fascicles. *Diaphragm* 6–8 cm from insertion to opening,

opening 13–14 cm in diameter, margin with pinkish zone, lower face except the marginal zone provided with ramenta c. 4–5 mm long. *Perigone lobes* 25–26 cm diameter, with yellowish whitish warts, which are laterally stretched, irregular shaped, partly connected and about 4 or 5 across in the middle part. *Disk* 12–13 cm diameter, processes 30–50. *Male flowers* with 26–38(–40) anthers.

Distribution — *Malesia:* Philippines (Mt Apo, Mindanao). No records during the 20th century.

13. Rafflesia tengku-adlinii Salleh & Latiff

Rafflesia tengku-adlinii Salleh & Latiff, Blumea 34 (1989) 111–116; Fl. Males. Bull. 11 (1995) 425–428. — Type: *Mat Salleh c.s. KMS 2180* (UKMS holo), Trus Madi Mts.

Mature *flower buds* about 13 cm in diameter. *Flowers* rather small, c. 20–24 cm in diameter. *Disk* about 6 cm diameter and neck of column 3 cm. *Perigone lobes* and *diaphragm* orange throughout including randomly distributed roundish warts, except near the opening, the diaphragm progressively dark reddish towards the centre. *Diaphragm* about 12.5 cm wide, with a 5 cm wide aperture. *Ramenta* slender, 3–5 mm long, partly branched and always with swollen apices, density somewhat reduced towards the opening and at the base of the tube, also present on the lower face of the diaphragm. *Disk* c. 7 cm diameter, flattened processes 25. *Male flowers* with 20 anthers.

Distribution — *Malesia:* Sabah, eastern slopes of Mt Trusmadi. Locality destroyed by loggers a few weeks after the plants were discovered. Later also found in the Gunung Lutong area at 600 m altitude inside the Yajasan Sabah concession.

Most likely the same species as the one seen by Meijer around 1964 near Telupid as a decaying flower.

Note — The measurements of the column, neck and disk were inferred from the drawing with the original description.

INCOMPLETELY KNOWN SPECIES

Rafflesia borneensis Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 47, pl.4. — Type: *Witkamp* collection (BO).

Relatively small *flowers* up to only 20–30 cm in diameter. *Flower tube* very flat and disk of column with a rather flat rim. *Ramenta* as far as seen in the specimen very short and sparse; Koorders described them as very short, rarely longer than 1 mm, with narrow pointed apex. He was unable to describe the perigone lobes and the diaphragm.

Distribution — Borneo, only once found in NE Kalimantan, Sekerat Mts, in 1917.

Habitat — At 600–700 m altitude, according to Coomans de Ruiter, Trop. Natuur 22 (1933) 166.

Note — Because of the flattened rim of the disk this species is rather similar to *R. rochussenii*. It is, however, distinguishable by the possession of the processes on the disk and by the very rudimentary ramenta, like those of *R. patma*. The remaining material in alcohol is very fragmentary and a good complete description is not possible.

Rafflesia ciliata Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 64, pl. 9. — Type: *Witkamp* collection from Sekerat Mts, NE Kalimantan, no material found in BO.

All we can learn about this enigmatic species from the original description, based on a bud of 17 cm diam., is that the perigone lobes have numerous dense warts, the ramenta are simple or branched, not swollen at apex, the lower face of the diaphragm has only bristles, no warts, and the disk has many processes, pointed at the apex. The hairy laminae between the anther cavities and the shape of the anthers and many other details given by Koorders are shared by most species of *Rafflesia* and are of no diagnostic importance.

A collection from the same huge general region of the Sekerat Mts was made on the Sangkulirang Peninsula by Kostermans, Sept. 1957, near Mapula(?) vilage. It consists of a male bud of 14 cm diameter with 40 anthers. This would make it likely that this specimen either belongs to *R. keithii* or that *R. arnoldii* occurs all the way from SW and C to NE Kalimantan. In case future fieldwork on the Sekerat Mts would show that *R. keithii* is common there we have enough circumstantial evidence that specimens of that species were described by Koorders under the names *R. witkampii* and *R. ciliata*. The latter species name could be excluded from priority because of the lack of a convincing type specimen. It is not possible to solve this puzzle without the collection of new evidence in the field.

Rafflesia titan Jack, Appendix Descr. Mal. Plants I (1821), reprinted in Hook. Comp. Bot. Mag. 1 (1835) 259.

The reason William Jack made his own description of *Rafflesia* and gave the name *R. titan* to the plants collected for Raffles and by Raffles and him in the province of Bengkulu before he died on 15 September 1822 was revealed in a letter he wrote in May 1821 to Wallich in Calcutta. The letter was reprinted by Burkill in a paper in J. Straits Br. Roy. Asiat. Soc. 73 (1916) 148–268, and contains the following statement: "You must observe that though labelled an appendix to the Malayan Miscellanies it has been kept back till we hear what is done at home about the great flower (*Rafflesia*). If it is brought forward in England then this is to be suppressed and not published; if no, then this may be used in the event of the French getting hold of it, as a proof of priority of publication."

From a letter he sent home 10 April 1820 [published by W.J. Hooker in Hook. Comp. Bot. Mag. 1 (1835) 135] we learn: "I lately sent to England a short account of some of my most interesting plants, to be noticed there in some way or other, including the sumatran gigantic flower, my two new Pitcher-Plants, the Camphor, the Sago and a new genus of mine, which Sir S. Raffles has forwarded for me, with the drawings of them, to Mr. Marsden, to make such use of them as he thinks best."

It must have taken sail ships at least three months to reach England from Sumatra.

On 30 June 1820 Robert Brown read his famous paper on *Rafflesia* at a meeting of the Linnean Society of London and an excerpt of this was published November or December of that year in the Dutch magazine Algemene Kunst en Letterbode vol. 2, nr. 3, and probably also in the German journal Flora.

From the correspondence between Dr. D.J. Mabberley, Dr John Bastin and myself in 1984 and 1985 no convincing evidence has been produced that Jack's Appendix reached England before the Brown paper came from the press in May or June 1821 and was distributed at least to various scientific quarters. The most likely date of publication of Brown's paper should be June 1821 at the latest, not July, the earliest month of arrival of two reprints in India [see Merrill, J. Arnold Arbor. 33 (1952) 203]. A copy sent to Brown by Jack was mailed in a letter dated 23 May 1821 according to Mabberley in an unpublished note, a part of the correspondence, in which he wrote me (4 March 1985): "it would be a service to the literate world to have this name (*R. arnoldii* R. Brown) fixed for all time."

To take any further doubt away we can also argue that we now know that before 1940 there were at least two species of *Rafflesia* known from Bengkulu (see under *R. gadutensis* in this treatment) and that the description by Jack is not fully convincing us that he had not mixed data from two species in his species description and that only for *R. arnoldii* we have very clear drawings and a type specimen available to proof its true identity.

Rafflesia tuan-mudae Becc., Atti Soc. Ital. Sc. Nat. 11 (1868) 197; Nelle For. Borneo (1902) 166, illus.; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 239, t. 27, f. 4, 5, 9; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 66; Pawozan, Family Tree, For. Dept. Sarawak Internal Newsl. 18 (1988) 3–7, col. phot. — Type: *Beccari s.n.* (FI-B).

Medium-sized flowers c. 44–56 cm diameter. Lower face of diaphragm and ramenta much like *R. arnoldii* but perigone tubes with only about 5–8 whitish warts across the broadest part, these relatively smaller than those of *R. gadutensis*. Number of anthers not known.

Distribution — *Malesia:* W Sarawak (Mts Pueh, Gading, Rara).

Habitat — As described by Beccari (1902) in lowland Dipterocarp forest.

Notes — 1. Beccari and Solms-Laubach did not have a sharp concept of this entity. Beccari himself [Nuovo Giorn. Bot. Ital. 7 (1875) 70–75] reduced his species to *R. arnoldii* Brown but later on left it to Solms-Laubach (l.c. 1891) to revive it, mainly based on the smaller size of the flowers and fewer blots across the perigone lobes.

2. Coomans de Ruiter collected *Rafflesia* in SW Borneo, later in Bogor identified as *R. tuan-mudae*, but the flowers illustrated by him are good matches of *R. arnoldii*. However, the smaller form described by Beccari was later also found on Mt Rara by Dr. J. Mogea (BO) and Dr. W.J.J.O. de Wilde (L). So it now appears to be a form restricted to three isolated mountains. As a widespread species *R. arnoldii* has greater variability in size and form than some species with smaller areas.

Rafflesia witkampii Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 61, pl. 7, 8. — Type: *Witkamp* collection, Sekerat Mts, NE Kalimantan (BO, in spirit).

This 'species' was described by Koorders merely on the basis of the study of a bud, 25 cm diameter, of a female flower. The column was expanded and a rupture in the tis-

sues between the annuli produced the 'wings' illustrated. Most likely the bud was left to dry out and later returned to a bottle with spirit. Several other 'distinctive' characters have no value because they were described from an immature bud. For the time being it is impossible to interpret this species as anything else than perhaps the female flower of *R. ciliata* Koord., collected at the same locality, an enigma itself. From the size of the bud we can exclude *R. pricei* as a possible identification. *Rafflesia keithii* would fit the size.

The species is possibly still present at the type locality though the site is doomed to disappear because of the planned establishment of a cement factory at that place. Other sites may still survive east of the Kutai National Park and in and around Sangkulirang. Ultimately the name may deserve priority over *R. keithii*.

RHIZANTHES

Rhizanthes Dumort., Anal. Fam. Pl. (1829) 14; Meijer & Veldkamp, Blumea 33 (1988) 329–342; Meijer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 561. — *Brugmansia* Blume in Van Hall, Bijdr. Natuurk. Wetensch. 2 (1827) 422, nom. illeg., non Pers. (1805). — *Zippelia* Rchb., Handb. Nat. Pfl.-Syst. (1837) 164, nom. illeg., non Blume ex Schult. & Schult. f. (1830). — *Mycetanthe* Rchb., Deut. Bot. Herb.-Buch (1841) 61, nom. illeg., superfl. — Type species: *Rhizanthes zippelii* (Blume) Spach.

Flowers unisexual or bisexual, buds pyriform, from a basal cupule attached to or arising from the roots or basal stem and aerial roots of the host, surrounded by three or four whorls of 5 scales, these sessile, imbricate, concave, more or less ovate, entire, brownish. *Perigone lobes* 16, valvate, with worm-like apices attached inside a cavity (crater) of the central column. *Anthers* in a ring around the lower margin of the column disk, about 38–50, each with 2 superimposed loculi. Male flowers with a rudimentary ovary, mature perigone tubes campanulate, radially striped in the center. *Fruits* hidden under dried-out flowers. *Seeds* with the same structure as those of *Rafflesia* [see Bouman & Meijer, Pl. Syst. Evol. 193 (1994) 187–212]. — **Fig. 10–12.**

Distribution — In *Malesia* 2 species (Sumatra, Peninsular Malaysia, Java, Borneo).

Ecology — The host of both species is in general *Tetrastigma papillosum* (Blume) Planch., sometimes also *T. leucostaphylum* (Dennst.) Alston ex Mabb. [= *T. lanceolarium* (Roxb.) Planch.].

Note — A very clever field investigation into the pollination of *Rhizanthes* (most likely *R. lowii*) in S Thailand and the Malay Peninsula (Perak) was reported by Bänziger (1996). He observed 900 visits of *Calliphoridae* (Bow flies) to 270 flowers and considers 6 species to be pollinators and the others non-pollinating visitors. His conclusion is that *Rhizanthes* just like *Rafflesia* mimics carrion in a pollination syndrome based on brood-site deception. Apparently eggs can be laid but the larvae starve to death. Insects are also lured to the nectaria at the base of the bayonets. As known to all observers, the flowers of *Rhizanthes* smell to the human nose much fainter than those of *Rafflesia*. See for other interesting details the original publication.

Reference: Bänziger, H., Nat. Hist. Bull. Siam Soc. 44 (1996) 113–142.

KEY TO THE SPECIES

1a. Flowers red-brown at anthesis, unisexual. Basal darker part of the bayonets covered with a velvety layer of c. 1.5 mm long, strongly branched antler hairs ..... **1. R. lowii**

b. Flowers white at anthesis, bisexual, male with rudimentary ovary, or male. Basal part of the bayonets with short hairs only once or twice branched or only curved at apex ..... **2. R. zippelii**

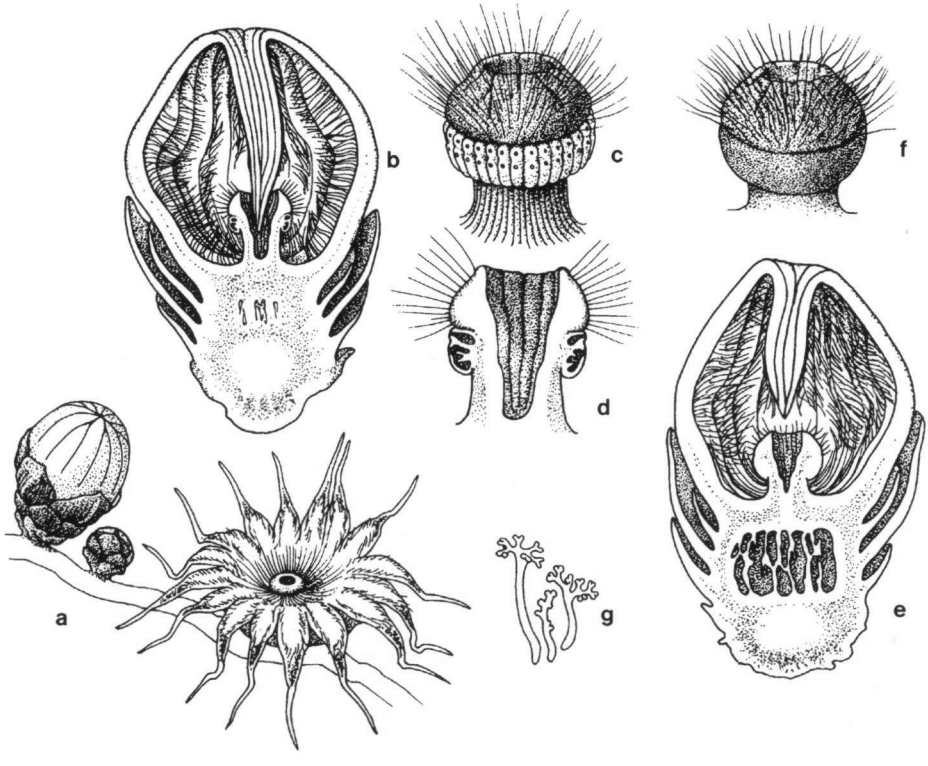

Fig. 10. *Rhizanthes lowii* (Becc.) Harms. a. Flowerbuds and open flower on stem or woody root of *Tetrastigma*. The mature bud left shows the cupula at base, the bracts, and the 16 valvate perigone lobes. The open flower shows the perigone and the narrow bayonets which in the bud were directed downwards and partly hidden in an apical cavity of the column; b. mature male flowerbud with rudimentary ovary; c. column of male flower, showing ring of anthers; d. section through the former; e. female flowerbud; f. column of female flower, stigmatic ring below the apex; g. ramenta from the glandular bases of bayonets from where they are often removed by frequent fly visits. Drawings by Janis Atlee, from photographs by W. Meijer, Kinabalu National Park, 1994.

1. Rhizanthes lowii (Becc.) Harms

Rhizanthes lowii (Becc.) Harms in Fedde, Rep. 36 (1934) 287; Corner & Watanabe, Illus. Guide Trop. Pl. (1969) 163. — *Brugmansia lowi* Becc., Atti Soc. Ital. Sc. Nat. 11 (1868) 198 (*'lowi'*); Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 101, t. 17, f. C – E; Merr., Enum. Born. Pl. (1921) 244; Ridl., Fl. Malay Penins. 3 (1924) 20, t. 137. — *Brugmansia zippelii* Blume var. *lowii* (Becc.) Hook. f. in DC., Prodr. 17 (1873) 113. — *Mycetanthe lowii* (Becc.) Hochr., Candollea 4 (March 1930) 188; Steenis, Bull. Jard. Bot. Buitenzorg III, 11 (June 1930) 18. — Type: *Low s. n. in Herb. Beccari* (FI holo; B).
More extensive list of references in Meijer & Veldkamp, Blumea 33 (1988) 335.

Flowers always unisexual, concolorous white to reddish (on Mt Leuser also with a white tube and brown lobes). Buds ovoid-pyriform, up to 12 by 7 cm; open flowers infundibuliform, 18–35 cm in diam. *Perigone lobes* 6–12 mm wide at base, gradually narrowed, basal hairy part c. 3 cm long, gradually narrowed into the geniculate, c. 2.5 cm by 1–2 mm apical appendage, the upper part of c. 6.5 cm without long hairs. *Perigone tube* inside long hairy below, the upper c. 2 cm with short hairs with an antler-like shape, male flowers with 50–60 lines, corresponding to the number of anthers. Central column c. 2 cm long, in female buds with a c. 0.5 by 1 cm diameter stipe, and a globular more or less depressed apex, 1–1.5 by 1.5–2 cm diameter, apical cavity c. 1 cm wide and deep. *Male flowers* with a c. 7 cm broad ring of 50–60 anthers around the base of the globular disk; stipe with c. 50–60 ridges; ovary rudimentary. Columnar disk of *female flowers* with a c. 7 mm wide stigmatic hairy zone along base; stipe not ridged; ovary c. 1.5 by 3 cm diam. *Fruit* not seen. — **Fig. 10, 11.**

Fig. 11. *Rhizanthes lowii* (Becc.) Harms. N Sumatra, Ketambe (*de Wilde 12148*). Photograph W.J.J.O. de Wilde, 1972.

Distribution — Sumatra (Aceh, Gajolands, Sibolangit, Bengkulu, Palembang, Lampong), Peninsular Malaysia (Pahang, Perak, Trengganu), Borneo (Sarawak, Sabah, W and E Kalimantan).

Habitat — Lowland Dipterocarp and hill forest, 200–1500 m altitude.

Ecology — Parasitic on *Tetrastigma papillosum* (Blume) Planch.

Notes — 1. Although in the footsteps of Beccari the epithet is often written as *lowi*; ICBN Art. 73.10 and Rec. 73 C 1 make it clear that *lowii* is the correct form.

2. Bänziger, Nat. Hist. Bull. Siam Soc. 43 (1995) 337–365 argues that there is only one species (*R. zippelii*) in this genus. However, he most likely never saw the real *R. zippelii*. He based his concept of it on the wrong identification by Meijer & Veldkamp (1988) of a specimen collected by Molesworth in a locality in Malaya which Bänziger also visited himself.

2. **Rhizanthes zippelii** (Blume) Spach

Rhizanthes zippelii (Blume) Spach, Hist. Nat. Vég. 10 (1841) 554; Backer & Bakh. f., Fl. Java 1 (1963) 166. — *Brugmansia zippelii* Blume in Van Hall, Bijdr. Natuurk. Wet. 2 (1827) 422; Miq., Fl. Ind. Bat. 1, 2 (1859) 684; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 94, t. 15, f. A–D. — *Zippelia brugmansia* Rchb., Handb. Nat. Pfl.-Syst. (1837) 164, nom. illeg., superfl. — *Mycetanthe zippelii* (Blume) Hochr., Candollea 4 (March 1930) 188; Steenis, Bull. Jard. Bot. Buitenzorg III, 11 (June 1930) 18. — Type: *Zippel s.n.* (L holo, spirit).

Brugmansia bakhuizenii Heinr., Denkschr. Akad. Wiss. Wien, Math.-Naturw. Kl. 78 (1906) 63, 66, t. 1, f. 1–4, t. 3, f. 3–5, 7, nom. prov., illeg.; Backer & Bakh. f., Fl. Java 1 (1963) 166, in obs. — Voucher: *Bakhuizen van den Brink s.n.* (IB).

More extensive list of references in Meijer & Veldkamp, Blumea 33 (1988) 339.

Flowers unisexual or bisexual, buds up to 10 by 5 cm, pinkish, smooth, at anthesis first concolorous white, later bright red or brown, 8–21 cm in diameter incl. the worm-like apical appendages. *Perigone lobes* c. 2.5 by 1.5 cm at base, free part 4.5–5 cm long (excl. the appendages), apex c. 0.5 cm thick; in upper c. 1.8 cm with short brown hairs with antler-shaped apices; lobes curved downwards touching the substrate, initially united at base in groups of 3 or 4, later free, splitting on the outside to c. 1.5 cm from the base of the tube, on the inside to c. 3 cm, forming a thin c. 1.5 cm long membrane. *Perigone tube* 2–2.5 cm long, inside with 46–55 brown lines around the column, fading out towards the base of the lobes; base and inside of the tube with 5–7 mm long hairs, apically slightly hooked; column c. 2 cm long, base narrow, c. 1 cm thick, head globular, 1.8–2 cm wide, apex purplish brown, hairy, crater 0.5–0.9 cm diam. *Anthers* 38–50. *Ovary* with stigmatic ring c. 0.5 cm high, white. *Fruit* subglobose, up to 6.5 cm diameter, brown, hidden by the dark-brown dried perianth. *Seeds* oblong, c. 0.75 by 0.3 mm, appendage oblong, about half as long as the seed. — **Fig. 12.**

Distribution — Sumatra (Aceh, W Sumatra, Bengkulu, Lampong), Peninsular Malaysia (Perak), Borneo (W Kalimantan, from Sabah and Sarawak no firm records), W Java (Ciapus canyon, Mt Salak).

Habitat — Primary or secondary forests, often along streams on deep alluvial soils, 500–1500 m altitude.

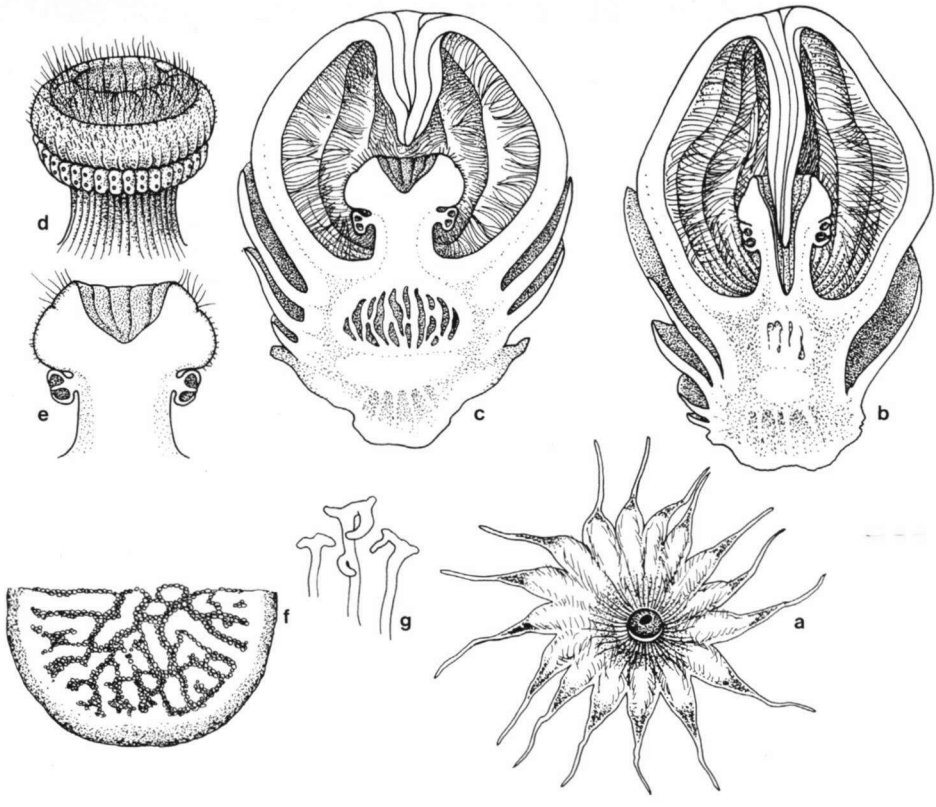

Fig. 12. *Rhizanthes zippelii* (Blume) Spach. a. Open flower, wine-red in colour; b. male flower in length section, ovary rudimentary, no trace of stigma ring around the column; c. bisexual flower in length section, ovary below the column which shows anthers as well as a stigmatic ring above them; d, e. detail of the column, with stigmatic ring; f. ripe fruit, partial cross section, thousands of seeds attached to the convoluted parietal placenta; g. ramenta at the base of the bayonets. Drawing by Janis Atlee: d, e after Blume, g after Heinricher; others from photographs made by W. Meijer in Sumatra, Ulu Gadut forest.

Ecology — Host is usually *Tetrastigma papillosum* (Blume) Planch., occasionally *T. leucostaphylum* (Dennst.) Alston ex Mabb. (names based on herbarium study by the present author). Van der Pijl [Trop. Natuur 22 (1933) 55] reported a species of *Villebrunea sp.* (*Urticaceae*) as host.

Notes — 1. Blume's original illustration of the flower reproduced repeatedly in the literature has given rise to some confusion because the flower shown had not yet fully expanded, the perianth lobes still sticking together in groups of 3 to 5.

The first illustrations of *Rhizanthes lowii* showed flowers with all perianth lobes free from each other. Heinricher [Denkschr. Akad. Wien, Math.-Naturw. Kl. 78 (1906) 63, 66, illus.], who found *R. zippelii* in its natural situation, was considering to describe it

as a new species *(R. bakhuizenii ?)*. Probably Blume's flower was produced in the laboratory after the host and buds were dug up from the jungle. There is nothing to indicate that the flower from Mt Salak represented a different species than those later discovered at all other localities.

2. Backer & Bakhuizen f. (1963) distinguished two forms: *R. zippelii* s.s. with white or flesh-coloured perianth, etc. from the Salak, and '*Brugmansia bakhuizenii*' with bright red perianth, etc. from Mt Gede, Cidadap, and Garut. The latter, however, is nothing else than the phase shown by flowers on the second or third day of flowering.

3. Since 1940 there have been no more reports of this species from Java (pers. obs., Kostermans pers. comm.). In October 1981 Meijer saw still some specimens of *Tetrastigma papillosum* in the steep Ciapus Canyon on Mt Salak. Cultivation and tree plantations had replaced the original forest at the margin of the canyon. No botanists have penetrated into the canyon in the past 60 years, but Meijer found in August 1996 that guides are leading parties into it.