

## A REVISION OF MITRASTEMA (RAFFLESIACEAE)

W. MEIJER<sup>1</sup> & J.F. VELDKAMP<sup>2</sup>

### SUMMARY

*Mitrastema* Makino (Rafflesiaceae), usually incorrectly called *Mitrastemon* Makino, has two species, one in Southeast Asia and one in Central and South America.

### INTRODUCTION

*Mitrastema* was described by Makino (1909) on *M.* (*'Mitrastemma'*) *yamamotoi* Makino. He intended to name the genus after the mitre-shaped staminal tube, as becomes evident when in 1911 he changed the name to *Mitrastemon*. This change is not allowed and *Mitrastemon* is a superfluous name. On the other hand, as Stearn (1973: 519) has pointed out, the Greek words 'stema' (thread, stamen) and 'stemma' (garland or wreath) are easily confused, and so *'Mitrastemma'* may be regarded as an orthographic error to be corrected under Art. 73.1 (Exx. 2, 3). *'Mitrastemon'* or *'Mitrastemma'* have been adopted in later publications, and even by the International Code of Botanical Nomenclature, where the name Mitrastemonaceae, invalid because it is based on an invalid name contrary to Art. 18.1, is conserved (1988: 104).

Since its description *Mitrastema yamamotoi* has become one of the most widely investigated taxa of the Rafflesiaceae. Especially Watanabe's papers on its morphology and biology (1933–1937) are masterpieces of devoted study; yet it is still not clear what the precise taxonomic position of the genus is and whether it really belongs to the Rafflesiaceae.

Some authors have regarded it as a distinct family, Mitrastemonaceae Makino (1911) (nom. cons.) (e.g. Cronquist, 1981; *'Mitrastemmataceae'*, Mabberley, 1987), others have treated it as Rafflesiaceae tribe Mitrastemateae (*'Mitrastemoneae'*). Makino's initial use in 1909 of this name (as *'Mitrastemmaeae'*) is invalid as no description in either Japanese or English was given (Dr. J.N. Westerhoven, Hirosaki, oral comm.). It was validated by Hayata (1913) (*'Mitrastemoneae'*).

Makino (1911: 252) even proposed it to represent a distinct order Mitrastemonales next to the Nepenthales, but he was apparently never followed in this. Although he called it *'series Mitrastemonales'* contrary to Art. 33.4 the name seems valid, if one accepts that *'series'* here is the latinization of the German *'Reihe'* of Art. 17.2.

Cronquist, hedging his bets, wrote "*'Mitrastemon'* has often been included in the Rafflesiaceae, to which it is evidently related. It is more primitive than the Rafflesia-

<sup>1</sup>) School of Biological Sciences, University of Kentucky, Lexington, KY 40506, U.S.A.

<sup>2</sup>) Rijksherbarium/Hortus Botanicus, P.O. Box 9514, 2300 RA Leiden, The Netherlands.

ceae in its hypogynous, perfect flowers, and its dome-like synandrium is more nearly comparable to that of *Prosopanche*, in the Hydnoraceae, than to anything in the Rafflesiaceae. Whether *Mitrastemon* should be included in the Rafflesiaceae or kept as a separate family is largely a matter of taste.”

To us Hayata (1913) has given overwhelming evidence that the genus belongs to Rafflesiaceae. He used the following arguments, extended by Watanabe (1933–1937) in great detail:

- 1) The endophytic body shows no characteristics different from those known from the Rafflesiaceae proper.
- 2) Bisexual flowers occur in *Rhizanthus zippelii* (Blume) Spach and *Bdallophyton oxylepis* (B.L. Rob.) Harms.
- 3) The tubular androecium is not completely unique to *Mitrastema*. In some species of the East African *Berlinianche* (Harms) Vattimo the stamens also form a tube around the pistil, e.g. in *B. aethiopica* (Welw.) Vattimo and *B. holtzii* (Engl.) Vattimo.
- 4) The superior ovary is an insufficient reason to exclude *Mitrastema* from the Rafflesiaceae. In many other families genera with superior as well as inferior ovaries have been admitted. Thus, not surprisingly, semi-inferior ovaries are known in some species of *Pilostyles* Guill., e.g. in *P. blanchetii* R. Br. (Gardner, 1844), *P. sessilis* Rose (1909), *P. thurberi* A. Gray (Gray, 1854), and *P. ulei* Solms-Laub. (Harms, 1935), at least in the female flowers.
- 5) All the detailed structures of the embryology, ovules, and seeds of *Mitrastema* agree well with those known for other species of Rafflesiaceae proper.

The multibranched, multiflowered inflorescences of *Cytinus* L. and *Bdallophyton* Eichl. seem primitive and so suggest that these may represent the genera closest to chlorophyllous ancestors of Rafflesiaceae. All other genera are single-flowered, though especially in *Apodanthes* Poit. and *Pilostyles* it might be considered that the inflorescences are buried inside the host and that their flowers pop up through the bark. In *Mitrastema* the flowers are still very gregarious, but they have become less so in *Rafflesia* Blume, *Rhizanthus* Dumort., and *Sapria* Griff.

*Mitrastema* also shares with other genera of the family the unicellular ovary with parietal placentas.

Watanabe (1936c) concluded that the stamen tube is derived from 15–20 (average 16) extrorse anthers, each originally with 4 pollen sacs and a connective extension. It is pushed off after the pollen has been shed by the growth of the pistil, ensuring cross-fertilization (the anthers are on the outside of the tube, while the stigma is inside it). Sexual reproduction is apparently obligatory (Watanabe, 1934a) but not always very successful. At higher latitudes the number of fertile fruits rapidly decreases.

He mentioned (1933a) that ripe fruits always become infested by a fungus. Its chlamydo-spores are concentrated around the micropylar area. He suggested (1936d) that the fungus might be fungicidal to other fungi. It may perhaps also take part in germination.

It is not clear how many species there actually are. Opinions vary between one to five, or even more.

Makino (1928), Matsuda ('Matuda') (1947), Van Royen (1963), and Hansen (1973) have defended the opinion that there is only one.

Corner & Watanabe (1969) depicted what they considered to be 5 species, and Corner (1978) could not identify the population from the Pinosok Plateau, Kinabalu, Sabah, which is now destroyed, so suggesting it was an undescribed one.

Watanabe (1934d, 1936a) described geographic variation in Taiwan and Japan in the number of pairs of scales. The southern localities usually had 6 pairs but towards the north there are only 4 or even 3. In Taiwan there were 8–12 pairs, while stems with many scales are more angular. There appears to be no correlation between the size of the flowers and the number of bracts. At some places flowers can be very small, but the plants have many pairs of bracts.

Intermediary forms between *Mitrastema kanehirae* and *M. yamamotoi* occur in the same area (Yamamoto, 1925; Watanabe, 1934d), while Van Royen (1963) reported that the differences between *M. kanehirae*, *M. kawa-sasakii*, and *M. yamamotoi* were found to exist in the abundant New Guinea material, which undoubtedly represented one species only.

Overall, a whole cline in size and number of pairs of scales seems to be present, and *M. kanehirae* appears to be only an extreme form of *M. yamamotoi*.

In Japan the plants show a seasonality in flowering, which is due to the presence of a dry season, in which they flower. Yamamoto distinguished a spring form (*M. yamamotoi*) and an autumn form (*M. kanehirae*). Palm (1934) observed that in North Sumatra, where a dry season is absent, flowering occurs all around the year (see Matsuda, 1947, for data on mean temperature and rainfall in Japan, Taiwan, and Sumatra). In New Guinea flowering seems to be seasonal, too (Van Royen, 1963).

One cause of the apparent variability is possibly due to edaphic and climatic factors. The depth of the roots of the hosts (Matsuda, 1947), how much litter is formed in the forests, mean temperature, start of the dry season, moisture, day length, etc. will no doubt influence the host and the development of its parasite. As some of these factors are linked with latitude, the clines could be explained. Matsuda (1947) suggested that the various forms are specific to their hosts. This seems an incorrect assumption, see for instance the observations by Rao & Balakrishnan (1972) on the Meghalaya population where 4 different species of 4 different families were being parasitised: *Castanopsis tribuloides* A.DC. (Fagaceae), *Elaeocarpus lancifolius* Roxb. (Elaeocarpaceae), *Engelhardtia spicata* Blume (Juglandaceae), and *Vernonia volkammeriifolia* DC. (Compositae).

Now that WM has been able to study more material than any previous student of the genus, we have come to the conclusion that the Southeast Asian specimens must be regarded as representatives of a single, variable species. This might seem to some a crude act of lumping, but there are too many overlaps, gradual transitions, and too narrow gaps in the characters. There are, as might be expected, local forms, or ecotypes, and in due course some of these might evolve further, if they have not been eradicated before, but at present, without looking at the field label, it is often impossible to say with certainty where a particular collection came from, and so to what 'species' it would belong.

An example is the treatment of the Sumatra population. Palm (1934) considered it to be conspecific with *Mitrastema yamamotoi*, Hayata (in litt. to Palm) identified it with *M. kawasasakii*, but Nakai (1941a, b) based a new species on it, *M. sumatranum*.

The Yunnan form (Li, 1975) fits in well as a range extension from Cambodia and Vietnam (Hansen, 1972, 1973).

Surprisingly, in 1924 a representative of the genus was discovered in the oak forests of Chiapas, Mexico. It was described as a distinct species, *M. matudae* Y. Yamamoto (1936, '*matudai*'), because of its much larger size, broadly triangular scales, and triangular fruits, and its conical, more or less pyramidal stigma. Matsuda (1947) gave a more extensive description, based on living material. At first sight this amphipacific distribution seems very strange, but there are quite a few similar ones of typical tropical genera. The explanation for such a curious disjunction remains unknown (see Van Steenis, 1962, for a list more than 20 genera). *Mitrastema matudae* appears quite distinct and must be regarded as a second species for the genus.

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### MITRASTEMA

*Mitrastema* Makino, Bot. Mag. Tokyo 23 (1909) (326) ('*Mitrastemma*'). — *Mitrastemon* Makino, Bot. Mag. Tokyo 25 (1911) 253, nom. inval. — Type species: *Mitrastema yamamotoi* Makino.

Parasites without chlorophyll, endoparasitic in roots, often inducing witches' brooms there, gregarious, often in a fairy ring around the host, breaking through its bark. Endophyte fungus-like. Basal part of exophyte a corky, lenticellate, pusticular cupule, mainly composed of host tissue, rim irregularly 4-lobed. *Stems* unbranched, terete to subquadrangular. *Leaves* sessile, scale-like, decussate, rarely whorled, in 3–7(–24) pairs, becoming larger upward, cream-coloured or milky yellowish-white at early flowering stage. *Pedicels* erect, terete or quadrangular. *Flowers* solitary, terminal, bisexual, protandrous, hypogynous, actinomorphic. *Perianth* persistent, much reduced, gamophyllous, collar-shaped, truncate to irregularly crenately 4-lobed. *Stamens* numerous, completely connate into a tube, widened at base, during early flowering stages surrounding the apex of the pistil but for a small aperture, caducous during anthesis, removed by the growing pistil; apical part (connective) sterile, below this with several series of vertical rings with c. 10 anthers each; anthers minute, with extrorse longitudinal slits. *Pollen* dicolpate. *Pistil* 1; ovary superior, ellipsoid, 1-locular, apex half conical with a narrow transverse groove below the style; placentas radial, 8–15(–20), unequally deeply intruding; ovules numerous, anatropous, unitegmic, tenuinucellar; style 1, slightly constricted, stigma thick, conical, sub-bilobed. *Fruit* becoming a slightly woody, berry-like capsule, dehiscing with a horizontal slit along the groove between the style and ovary. *Seeds* with a short funicle, sticky, testa hard, formed from the inner integument, yellowish to dark brown, reticulate because of collapsed cell walls when dry; endosperm a sweet jelly-like pulp, surrounding the embryo; embryo minute, undifferentiated, 4-celled.

Distribution — Species 2, one in Asia from India (Meghalaya) to S China (Yunnan), Japan, Ryukyu I., Taiwan, and Malesia (Sumatra, Borneo, New Guinea), one in South America, from Mexico (Chiapas) to Guatemala and NW Colombia.

Habitat — Endophytic body living in the roots of older trees of species mainly of Fagaceae (*Castanopsis*, *Lithocarpus*, *Quercus*, *Trigonobalanus*), infected roots swollen and growing near the surface with root witches' brooms. Endophytic body living like a mycelium, in early stages near the cambium, later included in older xylem.

Ecology – Seasonally flowering in subtropical areas, non-seasonally in tropical ones. Pollinated by flies (*Drosophila* sp.: Palm, 1934; Van Royen, 1963), *Chrysomya megacephala* (F.), a bee (*Apis* sp.), wasps [*Braconidae* sp., *Vespa magnifica nobilis* Sonan (Matsuda, 1947) that crawl over the anthers], a firefly (*Lampyridae* sp.) (Van Royen, 1963), and birds [e.g. *Zosterops (palpebrosus) japonicus* Temminck & Schlegel, 1847] which feed on the nectar excreted in the axils of the uppermost pairs of scales (Watanabe, 1934a). Seed dispersal most likely by these birds and small mammals.

Chromosomes –  $x = 20$  (Matsuura, 1935; Watanabe, 1936c).

#### KEY TO THE SPECIES

- 1a. Flowers c. 6 cm long. Staminal tube 20–28 mm long; anthers in a 6–12 mm broad ring. Ovary c. 16 by 15 mm; style c. 10 mm wide. Stigma 6–7 by 7–15 mm. – America ..... 1. *M. matudae*  
 b. Flowers 1.5–2 cm long. Staminal tube 14–20 mm long; anthers in a 2–5 mm broad ring. Ovary c. 8 by 3 mm; style 3–6 mm wide. Stigma 2–5 by 4–6 mm. – Asia ..... 2. *M. yamamotoi*

#### 1. *Mitrastema matudae* Y. Yamamoto

*Mitrastema matudae* Y. Yamamoto, Bot. Mag. Tokyo 50 (1936) 539 ('*Mitrastemon matudai*'). — Lectotype: *Matsuda* 38595 (TI holo; MEXU), Mexico, Chiapas Prov., Soconusco Dist., Escuintla Municipality, Mt Ovando, 1700 m, parasitic on *Quercus boqueronae* Trelease, 5 April 1936.

Plants 4–12 by 3–3.5 cm. Cupule 1–1.5 by 2–2.5 cm, margin weakly lobed. Stems c. 10 mm diameter. Leaves usually in 6 or 7 pairs, broadly to narrowly ovate, 13–30 by 10–25 mm, apex obtuse to apiculate. Flowers c. 6 cm long. Perianth 6–10 mm high. Staminal tube 20–28 mm long; anthers in a 6–12 mm broad ring. Ovary ellipsoid, c. 16 by 15 mm, style c. 2 by 10 mm, stigma 6–7 by 7–15 mm; placentas c. 15. Fruit up to c. 10 by 15 mm.  $2n = ? 63$

Distribution – South America: Mexico (Chiapas Prov.), Guatemala (Alta Vera Paz), Colombia (Dept. Antioquia).

Habitat – Montane rain or cloud forests, 1700–2500 m altitude.

Ecology – Parasitic on *Quercus boqueronae* Trelease.

Collector's note – Bracts and total plant white.

#### 2. *Mitrastema yamamotoi* Makino

*Mitrastema yamamotoi* Makino, Bot. Mag. Tokyo 23 (1909) (326), fig. — *Mitrastemon yamamotoi* Makino, Bot. Mag. Tokyo 25 (1911) 255, t. 7. — Syntypes: *Tashiro s.n.*, c. A° 1882, *Bando s.n.*, A° 1909, *H. Yamamoto s.n.*, A° 1907, 1908, 1911 (TI), Japan, Kyushu.

*Mitrastemon kawasasakii* Hayata, Bot. Mag. Tokyo 26 (1912) 112, fig. — *Mitrastemon yamamotoi* Makino var. *kawasasakii* Makino, J. Jap. Bot. 5 (1928) 18. — Type: *Kawakami & Sasaki s.n.* (TI holo), Taiwan, Monte Muto, 1250 m, Jan. 1911.

- Mitrastemon kanehirae* Y. Yamamoto, Bot. Mag. Tokyo 39 (1925) 142, f. 1–15 ('*kanehirai*'). — *Mitrastemon yamamotoi* Makino var. *kanehirae* Makino, J. Jap. Bot. 5 (1928) 18 ('*kanehirai*'). — Type: *Kanehira s.n.* (TI holo), Taiwan, Rangeshi Nantou, on roots of *Castanopsis jung-huhni* (Miq.) Markgr. or *Lithocarpus uraiana* (Hayata) Hayata, Oct. 1924.
- Mitrastemon cochinchinensis* Nakai, Icon. Pl. As. Or. 4 (1941) 306, t. 104. — Type: *Anonymus s.n.*, Institut des Recherches Agronomique de l'Indochine (TI holo), Cambodia, massif granite, 1700 m, Feb. 1930.
- Mitrastema sumatranum* Nakai [Icon. Pl. As. Or. 4 (1941) 306, nomen], Icon. Pl. As. Or. 4 (1941) 338, t. 113. ('*Mitrastemon sumatranus*'). — Type: *Jochems s.n.* (TI holo), Sumatra, Karo Mts, 1400 m, Aug. 1927.

Plants 2.5–15 by 3 cm. Cupule 1–2 by 0.5–2 cm, margin irregularly lobed. Stems 5–15 mm diameter. Leaves broadly to narrowly ovate, (4–)10–20(–28) by (5–)10–15(–25) mm, apex bluntly rounded. Flowers 1.5–2 cm long. Perianth 5–10 by 6–17 mm. Staminal tube tubular, 14–20 mm long; anthers in a 2–5 mm broad ring. Ovary ellipsoid, c. 8 by 3 mm; style ovoid-ellipsoid, 2–8 by 3–6 mm; stigma 2–5 by 4–6 mm. Fruit up to c. 20 by 10 mm.  $2n = 40$ .

Distribution — India (Meghalaya), Thailand (Loei), Cambodia, Vietnam (Dalat), China (Yunnan), Japan (Shikoku, Kyushu), Ryukyu I. (Amami I., Okinawa) (see map in Watanabe, 1937b), Taiwan; Malesia: Sumatra (Aceh, E Coast), Borneo (Sabah: Kinabalu), Papua New Guinea (Western Highlands, Eastern Highlands, Morobe, Milne Bay Prov.).

Habitat — In montane oak forests, 400–2000 m altitude.

Ecology — On *Castanopsis tribuloides* A.DC., *Elaeocarpus lancifolius* Roxb., *Engelhardtia spicata* Blume, and *Vernonia volkameriifolia* DC. in India (Rao & Balakrishnan, 1972); elsewhere on *Castanopsis* species, e.g. *C. acuminatissima* (Blume) A.DC., *C. cuspidata* (Thunb.) Schottky and its var. *sieboldii* (Makino) Nakai, *C. taiwaniana* Hayata, *Eugenia* sp., *Ilex integra* Thunb., *Limlia uraiana* (Hayata) Masamune & Tomiya, *Lithocarpus elegans* (Blume) Soepadmo, *L. kawakamii* Hayata, *Quercus glauca* Thunb., *Trigonobalanus verticillata* Forman. Locally abundant, growing in large patches, up to 2 m diameter.

Collector's notes — Plant white, brownish white, pink, 5–7 cm long, stem cylindrical to more or less quadrangular, c. 1 cm in diameter. Scales in 6–10 pairs, obconical, 1–2.5 by 0.8–2 cm, cream. Flowers with a fetid smell. Staminal column and ovary at first pink, later brown.

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## SPECIMENS SEEN

(Only numbered or dated collections could be included)

- Balakrishnan 34188: yam — Bando A° 1909: yam (T) — Boufford & Mitsuta 20128: yam — Breedlove 25400: mat; 34366: mat.  
 Core 510: mat — Cruttwell 1645-A: yam.  
 Elliott 1052: yam.  
 Harada 11//1912: yam; 3/1937: yam — Hartley 12100: yam — Hatusima 22806: yam — Hayata A° 1915: yam — Hayata & Ito 4/4/1914: yam — Honda 31/5/1939: yam; 18/8/1954: yam.  
 Jochems A° 1926: yam; 8/1927: yam (T).  
 Kanehira 10/1924: yam (T) — Kanehira & Sasaki 12/2/1918: yam — Kawakami & Sasaki 1/1911: yam (T) — Kimula 19/11/1921: yam — Kinabalu Park Naturalist A° 1983: yam.  
 Matsuda ('Matuda') A° 1924 (T): mat; 38595: mat (T) — Muramatsu 25/8/1937: yam.  
 NGF 14579 (Womersley & Millar): yam; 30726 (Streimann): yam.  
 Ohnuma 20/11/1913: yam — Ohwi & Akamoto 1482: yam.  
 Palm A° 1923: yam.  
 A. S. Rao 37958: yam; 38222: yam; 38223: yam; 38224: yam; 38225: yam; 38285: yam — van Royen 11039: yam; 15092: yam — RSNB 5746 (Chew & Corner): yam.  
 Shingu 2/1913: yam — Standley 91455: mat — Streimann 8486: yam — Suzuki 23/12/1931: yam; 14502: yam.  
 Tashiro A° 1882: yam; 25/1/1924: yam — Togashi 12/11/1912: yam — Tsai 58-8275: yam.  
 Vink 16402: yam; 16402-A: yam.  
 Wada et al. 100: yam — Watanabe 29/11/1934: yam; 27/2/1935: yam; 2/1936: yam — Womersley A° 1966: yam.  
 H. Yamamoto A° 1907: yam (T); A° 1908 (T): yam; A° 1911: yam (T) — Y. Yamamoto et al. 864: yam — Y. Yamamoto & Mori 2-3/11/1932: yam — Yamazaki 6981: yam; 26/12/1962: yam; 9/1/1964: yam; 20/11/1978: yam.