



A taxonomic revision of *Trigonostemon* (Euphorbiaceae) outside Malesia

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Key words

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Abstract The *Trigonostemon* species outside Malesia are taxonomically revised based on herbarium collections and fresh material. The research history in the concerning regions, i.e., the Indian subcontinent (including S India, Sri Lanka, Bangladesh and Myanmar), China, Thailand, Indochina, NE Australia and New Caledonia, is briefly summarised. A total of 32 species are accepted (including one doubtful species) and 17 names are newly treated as synonyms. *Trigonostemon montanus* is newly described for India. Regional identification keys, nomenclature, descriptions, geographic distributions and taxonomic notes are provided. Together with our previous work, the genus is now fully revised. A total of 59 species are accepted. A full identification list of all *Trigonostemon* collections seen is presented.

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INTRODUCTION

Trigonostemon Blume is a plant genus in the Euphorbiaceae. It is classified in the subfamily Crotonoideae (Wurdack et al. 2005) and includes four sections based on molecular, morphological and palynological evidence (Yu et al. 2019). *Trigonostemon* species often grow in lowland rainforests along rivers or coast lines. They are characterised by 5-merous colourful flowers and a connate androphore of 3 or 5 stamens. The genus originated in the SE Asian mainland (Yu & Van Welzen 2020) and has the highest diversity in W Malesia (Yu & Van Welzen 2018). However, its distribution also extends to S China, S India and Sri Lanka, and in scattered patches to E Malesia, NE Australia and New Caledonia (Govaerts et al. 2000). The Malesian species were revised (Yu & Van Welzen 2018, Yu et al. 2020), whereby historical literature was reviewed and useful characters for identification were discussed. This article is to revise the remaining species and present an identification list of this variable genus.

Balakrishnan & Chakrabarty (1991) rendered an exhaustive account of the research history and morphological characters of *Trigonostemon* in the Indian subcontinent (India, Sri Lanka, Bangladesh and Myanmar). With 13 species presented, this work demonstrates the authors' profound knowledge of the native taxa. Some of the points they discussed, for example, the use of venation patterns in the infrageneric classification, are supported by the molecular phylogeny (Yu et al. 2019). It is noteworthy that a disjunctive distribution of the genus exists in India: the plants are only present in the NE and S parts of the country.

For Indochina, a full revision of *Trigonostemon* is still lacking. The first batch of 15 species was presented by Gagnepain in 1922. One year later, he proposed a new genus *Prosartema* Gagnep. (Gagnepain 1924), mainly based on a difference from

Trigonostemon in the elongated anthers with a conical appendix. In the following year (Gagnepain 1925a), a new species was described for *Prosartema* and another new genus, *Poilaniella* Gagnep., was proposed. *Poilaniella* differs from *Trigonostemon* mainly in the cupular disc, sessile anthers and short cymes with non-fascicled flowers. These two genera, however, were both synonymised with *Trigonostemon* in later treatments (e.g., Airy Shaw 1978, Yu & Van Welzen 2018). Two more species were also described for *Trigonostemon* in the same year (Gagnepain 1925a). All these taxa (three genera and 20 species) were considered as endemic to Indochina at that time. Later in this year, Gagnepain (1925b) transferred *T. laoticus* Gagnep. to *Prosartema*, and newly recorded two *Trigonostemon* species originally only known for Thailand for the Indochinese flora. Therefore, a total of 22 species (18 under *Trigonostemon*, three under *Prosartema* and one under *Poilaniella*) were accepted for Indochina (Gagnepain 1925b), and this forms our basic knowledge of the plants in this area. Recently, four species were added to the Flora of Vietnam (Hô 1992) and one species was newly described (Tagane et al. 2017). Because Hô (1992) followed Airy Shaw's (1969) generic circumscription of *Trigonostemon* (for details see Yu & Van Welzen 2018), two species of *Tritaxis* Baill. (as *Trigonostemon annamensis* (A.Chev.) P.H.Hô (basinonym *Tritaxis annamensis* A.Chev. was not published) and *Trigonostemon gaudichaudii* (Baill.) Müll. Arg.) were also included in his work.

Thailand shares a large proportion of species with the adjacent areas. Only four species were newly described for Thailand (Craib 1911, 1924, Airy Shaw 1971). Another nine species were recorded for Thailand by Craib (1911) and Airy Shaw (1969, 1972). On the basis of Airy Shaw's (1972) treatment, Chantaranothai (2005) added one more species to the Flora of Thailand project; therefore, a total of 14 species (two endemic) were accepted for the Flora of Thailand (Chantaranothai 2007). Thailand and Indochina neighbour each other and it seems odd that the numbers of newly described species in the early years (before 1925) are in striking contrast (2 vs 24, respectively). This likely reflects a difference in the species concepts of the authors: Craib was seemingly more conservative than Gagnepain.

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In China, 13 species were newly described between 1909 and 1995 (Stapf 1909, Merrill 1922, 1930, 1932, Handel-Mazzetti 1932, Merrill & Chun 1935, Croizat 1940 (*Cleidion xyphophyloides* Croizat = *Trigonostemon xyphophyloides* (Croizat) L.K.Dai & T.L.Wu in Chun et al. 1963); Airy Shaw 1971, Chang 1983, 1989, Kiu 1995). *Trigonostemon fungii* Merr. was reduced to a form of *T. chinensis* Merr. by Chang (1989) and two more varieties were newly described by Kiu & Chen (1992). These taxa were studied and compiled in the Flora Reipublicae Popularis Sinicae (Kiu 1996). A total of 10 species and one variety were accepted, but *T. kwangxiensis* Hand.-Mazz. (including a variety) and *T. wui* H.S.Kiu were overlooked. All the taxa except for *T. thyrsoides* Stapf were considered endemic then. However, Li et al. (2006) reduced the number of species to eight only. Some names were treated as synonyms of taxa that were known for Indochina, Thailand and even Myanmar. Furthermore, Li & Gilbert (2008) synonymised *T. leucanthus* Airy Shaw with *T. albiflorus* Airy Shaw. Eight species were accepted in the Flora of China (Li & Gilbert 2008), of which only one was considered as endemic.

The distribution of *Trigonostemon* also extends to the southeast of the Malay Archipelago. One species in NE Australia (*T. inopinatus* Airy Shaw 1976) and one in New Caledonia (*T. cherrieri* Veillon 1992) were described.

Key to the species of India (including Andaman & Nicobar Islands), Sri Lanka and Bangladesh

(couplet 5 partly according to Balakrishnan & Chakrabarty 1991; couplet 6 partly according to Talukdar et al. 2015)

1. Venation pinnate 2
1. Venation triplinerved 6
2. Flowers partly (at least staminate ones) cauliflorous 3
2. Flowers never cauliflorous, inflorescences axillary or terminal 4
3. Leaf blade elliptic to oblong, lower part narrow-rounded; petals orange 2. *T. aurantiacus*
3. Leaf blade oblanceolate, lower part cuneately narrowed; petals purple 26. *T. semperflorens*
4. Pistillate sepals without a gland or appendage outside. — Great Nicobar island 29. *T. villosus* var. *nicobaricus*
4. Pistillate sepals (check multiple sepals) with a gland or appendage outside. — Travancore, Sri Lanka 5
5. Petals bilobed; stigmas twice-bifid. — Sri Lanka 7. *T. diplopetalus*
5. Petals not bilobed; stigmas bifid. — Travancore, Sri Lanka 21. *T. nemoralis*
6. Inflorescences shorter than 2 cm 19. *T. montanus*
6. Inflorescences longer, up to 12 cm long 30a. *T. viridissimus* var. *viridissimus*

Key to the species of Myanmar

1. Venation pinnate 2
1. Venation triplinerved 7
2. Petioles shorter than 3.5 cm 3
2. Petioles of at least some leaves longer than 3.5 cm 4
3. Flowers mostly cauliflorous, inflorescences cymes or thyrses (with side branches); pistillate sepals crescent; fruits smooth 9. *T. flavidus*
3. Flowers never cauliflorous, inflorescences axillary or terminal, racemes or racemose thyrses (without side branches); pistillate sepals not crescent, fruits more or less warty 17. *T. longifolius*
4. Inflorescences paniculate. — Mandalay 23. *T. philippinensis*

4. Inflorescences racemes or racemose thyrses. — Tenasserim, Amherst 5
5. Pistillate sepals not crescent. — Amherst 18. *T. malaccanus*
5. Pistillate sepals crescent. — Tenasserim 6
6. Disc of 5 glands or lobes; pistillate sepals fringed with capitate glands 11. *T. heteranthus*
6. Disc annular; pistillate sepals with a mostly entire margin but with 2 teeth near apex 15. *T. lanceolatus*
7. Staminate flower buds globose; fruits hirsute. — Sagaing, Kachin 24. *T. quocensis*
7. Staminate flower buds conical; fruits glabrous. — Mergui, Tenasserim 30a. *T. viridissimus* var. *viridissimus*

Key to the species of China

1. Leaf blades pubescent above 2
1. Leaf blades glabrous to slightly pubescent above 4
2. Venation pinnate; petals reddish purple to black, flowers mostly cauliflorous 9. *T. flavidus*
2. Venation triplinerved or palmate; petals yellow to orange; flowers never cauliflorous 3
3. Disc glabrous; fruits 1.05–1.3 cm diam, smooth 1. *T. adenocalyx*
3. Disc pubescent; fruits c. 3 cm diam, warty 27. *T. tuberculatus*
4. Domatia present on the lower surface of at least some leaves 10. *T. fragilis*
4. Domatia absent 5
5. Venation pinnate 6
5. Venation triplinerved 8
6. Petioles of at least some leaves longer than 3.5 cm 23. *T. philippinensis*
6. Petioles shorter than 3.5 cm 7
7. Petals dark purplish; staminate inflorescences racemose thyrses, never cauliflorous 17. *T. longifolius*
7. Petals orange; staminate inflorescences condensed cymes or thyrses, always cauliflorous 31. *T. xyphophyloides*
8. Inflorescences (when mature) often longer than 13 cm 9
8. Inflorescences up to 13 cm long 10
9. Petals white; style often indistinct, 0.1–0.2 mm long 8. *T. eberhardtii*
9. Petals yellow to orange; style 0.2–0.7 mm long 30. *T. viridissimus*
10. Translucent (oil?) dots often present in green parts; leaf blades indistinctly triplinerved; inflorescence axis very slender, up to 0.5 mm diam; often only a few flower buds present in the inflorescences in herbarium specimens. — Guangxi 3. *T. bonianus*
10. Translucent (oil?) dots absent in green parts; leaf blades distinctively triplinerved; inflorescence axis stronger, up to 1 mm diam; often a large number of flowers present in the inflorescences in herbarium specimens. — Yunnan 16. *T. lii*

Key to the species of Thailand

1. Petioles shorter than 3.5 cm 2
1. Petioles of at least some leaves longer than 3.5 cm 12
2. Leaf blades pubescent above 3
2. Leaf blades glabrous to slightly pubescent above 4
3. Indumentum of only simple hairs; flowers mostly cauliflorous 9. *T. flavidus*
3. Indumentum of simple and stellately bundled hairs; flowers never cauliflorous 25. *T. reidioides*

4. Petals yellow, orange or light pink 5
4. Petals white, dark pink, dark red to purplish black 7
5. Staminate flowers cauliflorous; filaments fully connate; anthers divaricate at apex 2. *T. aurantiacus*
5. Flowers never cauliflorous; filaments often with a free part; anthers not divaricate 6
6. Translucent (oil?) dots absent in green parts; leaves glabrous on the lower surface; petals bilobed 14. *T. laevigatus*
6. Translucent (oil?) dots present in green parts; leaves sparsely pubescent on the lower surface; petals with an entire margin 30a. *T. viridissimus* var. *viridissimus*
7. Stamens 5 8
7. Stamens 3 9
8. Inflorescences often longer than 1.5 cm (staminate 4–8 cm, pistillate 1–15 cm) 4. *T. capillipes*
8. Inflorescences shorter, up to 1.5 cm long 22. *T. pachyphyllus*
9. Disc annular 10
9. Disc of 5 glands or lobes 11
10. Indumentum of only simple hairs; inflorescences racemes or racemose thyrses 17. *T. longifolius*
10. Indumentum of simple and stellately bundled hairs; inflorescences paniculate thyrses 25. *T. reidioides*
11. Pistillate sepals fringed with capitate glands; fruits glabrous 13. *T. kerrii*
11. Pistillate sepals with an entire margin; fruits pubescent 20. *T. murtonii*
12. Inflorescences paniculate thyrses (with side branches) 13
12. Inflorescences racemose thyrses (without side branches) 15
13. Filaments fully connate; anthers divaricate at apex 23. *T. philippinensis*
13. Filaments often with an apical free part; anthers not divaricate 14
14. Petals white (or rarely yellow), staminate flower buds often conical; fruits glabrous 8. *T. eberhardtii*
14. Petals yellow, staminate flower buds globose; fruits hirsute 24. *T. quocensis*
15. Stamens 5 28. *T. verticillatus*
15. Stamens 3 16
16. Pistillate sepals accrescent 15. *T. lanceolatus*
16. Pistillate sepals not accrescent 18. *T. malaccanus*

Key to the species of Indochina (Laos, Cambodia, Vietnam)

(*Trigonostemon adenocalyx* is not included in the key, because there is no certain collection record for this area)

1. Venation pinnate 2
1. Venation triplinerved 7
2. Petioles shorter than 3.5 cm 3
2. Petioles of at least some leaves longer than 3.5 cm 6
3. Leaves pubescent above; flowers mostly cauliflorous 9. *T. flavidus*
3. Leaves glabrous to slightly pubescent above; flowers never cauliflorous 4
4. Inflorescence longer, up to 30(–55 in extreme cases) cm long; disc annular 17. *T. longifolius*
4. Inflorescence up to 11.2 cm long; disc of 5 glands or lobes 5
5. Pistillate sepals fringed with capitate glands; fruits glabrous 13. *T. kerrii*
5. Pistillate sepals with an entire margin; fruits pubescent 20. *T. murtonii*

6. Inflorescences racemose thyrses; pistillate sepals accrescent; fruits densely hirsute, smooth 15. *T. lanceolatus*
6. Inflorescences paniculate; pistillate sepals not accrescent; fruits glabrous, warty 23. *T. philippinensis*
7. Indumentum of simple and stellately bundled hairs 25. *T. reidioides*
7. Indumentum of only simple hairs 8
8. Domatia present on the lower surface of at least some leaves 10. *T. fragilis*
8. Domatia absent 9
9. Translucent (oil?) dots absent in green parts 16. *T. lili*
9. Translucent (oil?) dots present in green parts 10
10. Petals white 8. *T. eberhardtii*
10. Petals yellow to orange 11
11. Inflorescence axis very slender, up to 0.5 mm diam; often only very few flower buds present in the inflorescences in herbarium specimens 3. *T. bonianus*
11. Inflorescence axis stronger, up to 2 mm diam, often a large number of flowers present in the inflorescences in herbarium specimens 12
12. Staminate flower buds globose; fruits hirsute 24. *T. quocensis*
12. Staminate flower buds conical; fruits glabrous 13
13. Fruits more or less warty 5. *T. capitellatus*
13. Fruits smooth 30. *T. viridissimus*

TAXONOMY

Throughout this part, an asterisk (*) refers to a specimen seen as image. The sections, as defined by Yu et al. (2019), are indicated for all species: sect. *Trigonostemon*, sect. *Pycnanthera* Benth., sect. *Spinipollen* R.Y.Yu & Welzen and sect. *Tylosepalum* (Kurz) Benth. For the generic description and a discussion of the characters, see Yu & Van Welzen (2018).

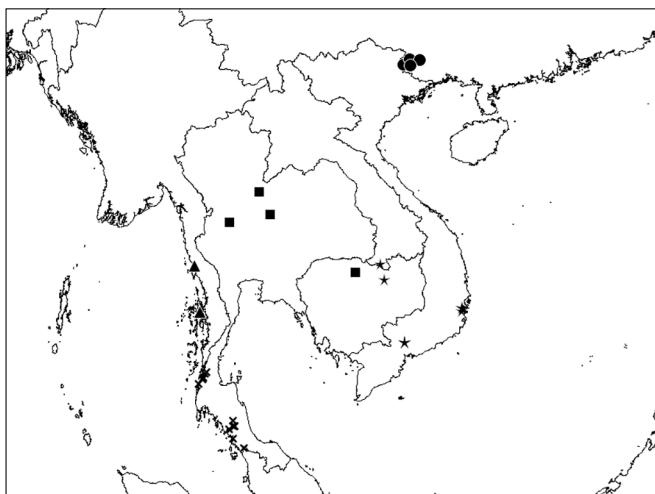
1. *Trigonostemon adenocalyx* Gagnep. — sect. *Tylosepalum*

— Map 1

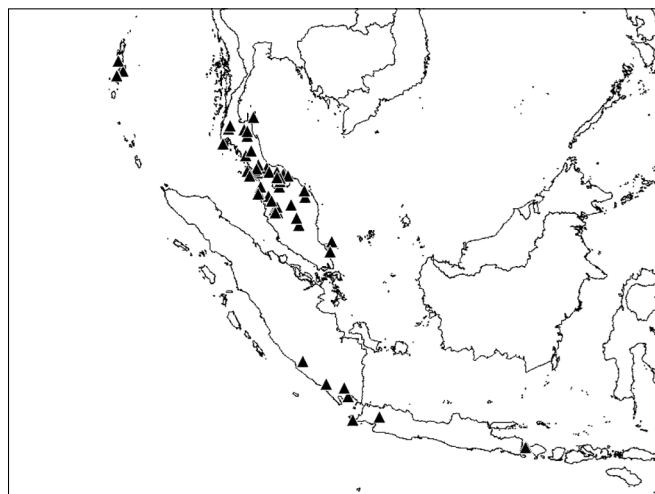
Trigonostemon adenocalyx Gagnep. (1922) 747; (1925b) 319. — Type: Unknown collector (P, barcode P00717084), Indochina?

Trigonostemon lutescens Y.T.Chang & J.Y.Liang in Chang (1983) 173. — Type: Longgang Exped. 12083 (IBK, barcodes IBK00169526, IBK00190787), China, Guangxi, Longgang Natural Reserve.

Shrubs, 0.4–1.2 m tall; flowering branches 1.1–3.5 mm diam, densely pubescent. Bark 0.1–0.2 mm thick, pale to dark brown; wood pale yellow. Stipules subulate, 0.4–0.7 mm long, often pubescent at base. Leaves: petiole terete but grooved above, 1–7.2 cm long, 1–2.3 mm diam, densely pubescent; blade elliptic, 9.5–28.6 by 3.5–11.7 cm, chartaceous, base acute to rounded, 2 adaxial glands present, margin distantly serrate, teeth falcate to glandular, apex acuminate, upper surface rough, with very small glandular protrusions spreading over the blade giving a sandpaper touch, both surfaces pubescent; venation triplinerved, midrib slightly raised above and elevated and pubescent beneath, secondary veins 7–12 pairs, connected along margin, tertiary veins scalariform, veinlets reticulate. Inflorescences bisexual, terminal or axillary panicles; main axis terete, 9–26 cm long, 1–1.9 mm diam, densely pubescent; bracts lanceolate to linear, 1–25 by 0.3–4 mm, pubescent. Staminate flowers 5–8.5 mm diam; buds conical; pedicel 4.7–6 mm long, 0.15–0.25 mm diam, pubescent; sepals elliptic, 1–2 by 0.5–1.4 mm, base connate, margin entire, apex acute to rounded, sometimes with a notch and an adaxial gland, slightly pubescent outside; petals flabellate, 4–7.2 by 1.7–4.5 mm, base claw-like, apex rounded, yellow to orange, glabrous; disc annular, 0.2–0.3 mm wide; stamens 3, androphore 0.9–1.7 mm



Map 1 Distribution of *Trigonostemon adenocalyx* Gagnep. (●), *T. capillipes* (Hook.f.) Airy Shaw (x), *T. capitellatus* Gagnep. (★), *T. heteranthus* Wight (▲) and *T. kerrii* Craib (■).



Map 2 Distribution of *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl.

long, 0.15–0.2 mm diam, free part of filaments 0.3–0.5 mm long, anthers ellipsoid, 0.5–0.6 mm long. *Pistillate flowers* c. 8 mm diam; buds conical; pedicel 1–1.5 cm long, 1–1.1 mm diam, pubescent; sepals lanceolate, 3–7 by 1–1.8 mm, apex acuminate; petals as staminate flowers; disc annular, c. 0.5 mm wide; ovary 0.9–1.2 mm diam, glabrous, style absent, stigmas 0.7–1.2 mm long, apically not bifid but thickened. *Fruits* 1.05–1.3 cm diam, glabrous, smooth, sometimes marbled; pedicel 0.8–1.7 cm long, 1.3–1.7 mm diam (apex); sepals persistent, very slightly or not accrescent; columella 4.5–6 mm long. *Seeds* not seen.

Distribution — China (Guangxi), Indochina (?).

Habitat & Ecology — In forests, growing on limestone. Elevation: 280–400 m. Flowering: April to May; fruiting: April and August.

Notes — 1. The species resembles *T. viridissimus* (Kurz) Airy Shaw var. *elegantissimus* (Airy Shaw) Airy Shaw in the large paniculate inflorescences and the conical flower buds, but the leaves contain small glandular lumps on the upper surface, which give a sandpaper touch.

2. The distribution of the species in Indochina is only known from the type specimen. The collecting location of the type specimen is uncertain (marked as 'Indo-Chine?' on the sheet). As we doubt the presence in Indochina the species is not listed in the key to the species in Indochina.

2. *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl. — sect. *Tylosepalum* — Map 2

Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl. (1900) 284; Pax & K. Hoffm. (1911) 93; (1931) 170; Jabl. (1963) 164, in obs.; Airy Shaw (1969) 126; (1972) 345, f. 11; Whitmore (1973) 136; Airy Shaw (1974) t. 3721; (1981) 352; Chantar. (2007) 576; R.Y. Yu & Welzen (2018) 187, f. 1. — *Tylosepalum aurantiacum* Kurz ex Teijsm. & Binn. (1864) 50. — *Codiaeum aurantiacum* (Kurz ex Teijsm. & Binn.) Müll.Arg. (1866) 1118. — Lectotype (designated by Yu & Van Welzen 2018): *Teijsmann s.n.* (L, barcode L.2260196), Indonesia, Java, cultivated in Bogor Botanical Garden (originally from Bangka?).

Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl. var. *ruberiflorus* N.P.Balakr. & Chakrab. (1984a) 169; Chakrab. (1985) 498. — Type: Ansari 1361 (holo CAL (1361A), barcode CAL0000023655; iso PBL (1361B–F), not seen), India, South Andamans, Havelock Islands.

Description & Taxonomic notes — See Yu & Van Welzen 2018.

Distribution — India (South Andamans), Thailand, Malay Peninsula, Sumatra, Java, Bali.

3. *Trigonostemon bonianus* Gagnep. — sect. *Tylosepalum* — Map 3

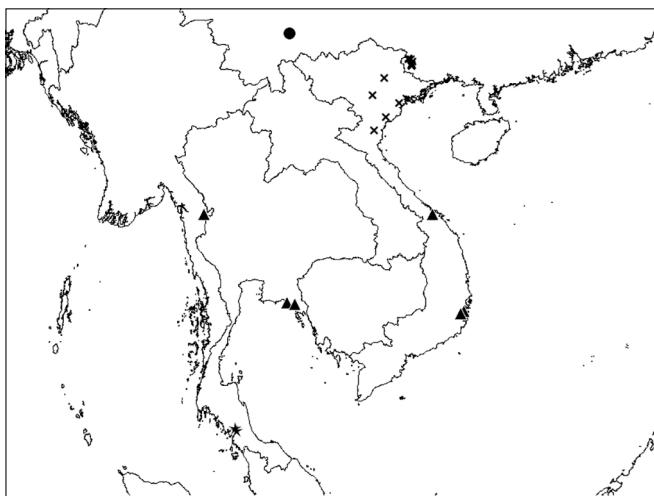
Trigonostemon bonianus Gagnep. (1922) 747; (1925b) 314; P.T.Li et al. (2006) 118; P.T.Li & M.G.Gilbert (2008) 274. — Lectotype (designated by Li et al. 2006): *Bon* 718 (P, barcode P00717086), Vietnam, Mount Trui.

Trigonostemon petelotii Merr. (1924) 425. — Type: *Pételot* 795 (A, barcode A00048876, P, barcodes P00648663, P00648664, UC*, barcode UC223795), Vietnam, Cho-Ganh.

Trigonostemon filipes Y.T.Chang & S.L.Mo in Chang (1989) 149; H.S.Kiu (1996) 169. — Type: *Longgang Exped.* 12240 (holo IBK, barcode IBK00169515; iso MO, barcode MO934096), China, Guangxi, Longgang Natural Reserve.

Trigonostemon kwangsiensis Hand.-Mazz. var. *viridulus* H.S.Kiu in Kiu & Chen (1992) 211. — Type: *Liang* 66719 (holo IBSC, barcode IBSC0306903; iso IBK, barcodes IBK00169523, IBK00169525), China, Guangxi, Longzhou, Shangjin, Longhushan.

Shrubs, 0.5–3 m tall; flowering branches 1–2 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts. *Bark* c. 0.1 mm thick, white when young, dark brown to black when mature; wood pale yellow. *Stipules* subulate, 0.3–0.9 mm long, caducous, pubescent at base. *Leaves*: petiole terete but grooved above, sometimes thickened at apex and base, 0.4–4 cm long, middle part 0.6–1.1 mm diam, pubescent; blade elliptic to oblong, 5.5–16 by 1.7–6.1 cm, somewhat thin-chartaceous, base acute to rounded, 1–2 pairs of adaxial glands present, often caducous, margin distantly serrate, teeth falcate, apex acuminate to caudate, upper surface glabrous or glabrescent, lower surface sparsely pubescent; venation indistinctively triplinerved, midrib slightly raised above and distinctively elevated and pubescent beneath, secondary veins 5–8 pairs, connected along margin, tertiary veins scalariform, veinlets reticulate, sometimes obscure. *Inflorescences* bisexual, often terminal, paniculate thyrses, often only a few flower buds present in the inflorescences in herbarium specimens; main axis terete, 3–13 cm long, (0.2–)0.4–0.5 mm diam, often slightly pubescent; involucral bracts as stipules; bracts linear to lanceolate to triangular, 0.2–3.5 by 0.2–0.6 mm, pubescent. *Staminate flowers* (bud) c. 2 mm diam; pedicel 0.8–3.9 mm long, 0.15–0.2 mm diam, glabrous to slightly pubescent; sepals elliptic to ovate, 0.7–1.5 by 0.3–1 mm, base connate, margin entire, apex acute, sometimes with a notch and/or an adaxial gland, pubescent outside; petals orbicular, 1.3–1.6 by 1–1.3 mm, yellow, apex rounded, glabrous; disc annular, margin undulate, c. 0.3 mm wide; stamens 3, androphore very short, indistinct, anthers globose to ellipsoid, 0.5–0.6 mm long. *Pistillate flowers* c. 8 mm diam; pedicel slightly thickening toward apex, 4.8–11.3 mm



Map 3 Distribution of *Trigonostemon bonianus* Gagnep. (x), *T. lanceolatus* (S.Moore) Pax (▲), *T. pachyphyllus* Airy Shaw (★) and *T. tuberculatus* F.Du & Ju He (●).

long, apically 0.6–0.9 mm diam when flowering, pubescent; sepals elliptic, 2–2.9 by 1–1.3 mm, apex acute, sometimes with a notch and an adaxial gland; petals as staminate flowers; disc annular, c. 0.4 mm wide, margin undulate; ovary c. 2.2 mm diam, glabrous, style c. 0.3 mm long, stigmas c. 0.5 mm long, not bifid. *Fruits* 0.8–1.1 cm diam, glabrous; pedicel 1.2–2.2 cm long, 1.2–1.5 mm diam (apex); sepals persistent but not accrescent; wall 0.3–0.5 mm thick, exocarp partly detaching; columella 5.7–7.7 mm long. *Seeds* 6.3–6.7 mm diam, marbled; hilum rhombic, 0.9–1.3 by 0.7–0.9 mm.

Distribution — China (Guangxi), Vietnam.

Habitat & Ecology — In forests, growing on limestone. Elevation: 160–650 m. Flowering: March to May, August to October; fruiting: May, August, November.

Note — The species has a unique spotting character: the inflorescences have a long (often more than 1/2 length of the whole inflorescence) and very thin peduncle without side branches.

4. *Trigonostemon capillipes* (Hook.f.) Airy Shaw — sect. *Trigonostemon* — Map 1

Trigonostemon capillipes (Hook.f.) Airy Shaw (1967) 413; (1972) 345; Whitmore (1973) 135; Airy Shaw (1975) 202; R.I.Milne (1995) 28, in key, 29, in key, 45; Chantar. (2005) 24; (2007) 576; R.Y.Yu & Welzen (2018) 191. — *Dimorphocalyx capillipes* Hook.f. (1887) 404; Pax & K.Hoffm. (1911) 33; Ridl. (1924) 266. — Type: Lobb s.n. (K, barcode K000894763), Singapore.

Description & Taxonomic notes — See Yu & Van Welzen 2018.

Distribution — Thailand (Trang, Ranong, Satun), Malay Peninsula (Perlis, Singapore).

5. *Trigonostemon capitellatus* Gagnep. — sect. *Tylosepalum* — Map 1

Trigonostemon capitellatus Gagnep. (1922) 748; (1925b) 311. — Lectotype (designated here): Pierre 1323 (P, barcode P00717092; iso K, barcode K000959315, P, barcodes P00717090, P00717091, US00433339), Vietnam, Bien Hoa, towards Dongnai river near Tri Huyen. — Other syntypes: Thorel s.n. (P, barcode P00717089), Laos, île de Khon; Pierre 472 (P, barcode P00717093), Vietnam, Bien Hoa, towards Dongnai river near Tri Huyen.

Trigonostemon cochinchinensis Gagnep. (1922) 748, syn. nov.; (1925b) 311. — Type: Pierre 1869 (K, barcode K000959316, P, barcodes P00717094, P00717095, P00717096), Vietnam, Bao Chiang.

Trigonostemon thorelii Gagnep. (1922) 755, syn. nov.; (1925b) 315. — Type: Thorel 2264 (A, barcode A00048877, P, barcodes P00648671, P00648672, P00717148), Laos, Stung Tréng à Kong.

Trigonostemon verrucosus J.J.Sm. (1924) 97, syn. nov. — Type: Bogor Botanical Garden VIII.E.16 (BO, sheets no. BO1298241, BO1298242, BO1298243, IBSC, barcode IBSC0306957, K, barcode K000959299, L, barcode L.2258669, SING, U, barcode U0002105), Java, cultivated in Bogor Botanical Garden.

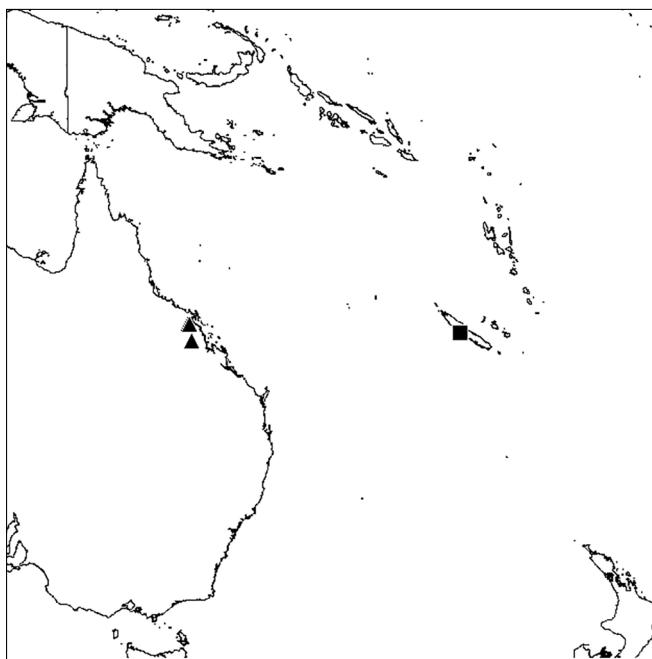
Shrubs, 1.5–3 m tall, dbh 2–3 cm; flowering branches 1.3–3.7 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts. *Outer bark* 0.1–0.2 mm thick, very finely roughened, brown, grey or black; inner bark 0.1–0.2 mm thick, dark red; wood pale yellowish, pith sometimes hollow. *Stipules* very small, often indistinct, pointing or subulate, 0.2–0.4 mm long, pubescent at base, caducous. *Leaves*: petiole terete but flat or slightly furrowed above, 0.3–2.3 cm long, 0.6–1.5 mm diam, pubescent; blade elliptic to oblong, 6–17.6 by 2–6.2 cm, chartaceous, base acute to rounded, 2 adaxial glands present, margin entire, apex acuminate to slightly caudate, upper surface glabrous, dark glossy green, lower surface more or less pubescent especially along venation and margin, bright light green; venation distinctly triplinerved, midrib and basal secondary veins slightly raised above, distinctly elevated beneath, other secondary veins 3–6 pairs, veinlets reticulate, sometimes obscure. *Inflorescences* bisexual, often axillary panicles; main axis up to 21 cm long, 0.5–1 mm diam, green, pubescent; bracts lanceolate, up to 3 by 0.5 mm, pubescent. *Staminate flowers* 3.5–5.5 mm diam; buds conical; pedicels 2.5–4.4 mm long, 0.15–0.3 mm diam, glabrescent; sepals elliptic to somewhat rectangular, 0.6–0.8 by 0.5–0.7 mm, apex truncate or slightly emarginate, glabrescent outside, with an apical gland outside; petals obovate, 2–3.2 by 1.2–1.7 mm, pale light to dull ochre-yellow, contort, apex rounded, glabrous; disc annular, 0.2–0.3 mm wide, 0.5–0.7 mm diam, glossy dark yellow, margin undulate, glabrous; stamens 3, androphore erect, 0.7–1.2 mm long, 0.1–0.15 mm diam, white, trifid at apex, free filament part 0.2–0.3 mm long, white, anthers free, subglobose, 0.35–0.6 mm long, cream. *Pistillate flowers* c. 5 mm diam; buds conical; pedicels as staminate flower but thickening toward apex, 5–7 mm long, apically 0.5–0.6 mm diam when flowering, accrescent up to 1.5 cm long and 1.5 mm diam in fruit; sepals as in staminate flowers but sometimes lanceolate, apex sometimes acute, sometimes with more hairs, especially near gland; petals as staminate flowers but caducous when fruiting; disc as in staminate flowers; ovary 0.7–0.8 mm diam, glabrous and sometimes gibbose, style 0.1–0.2 mm long, stigmas 0.6–1 mm long, apically very slightly bifid and thickened. *Fruits* 0.95–1 cm diam, glabrous, more or less warty; sepals persistent but not accrescent; wall 0.3–0.5 mm thick, exocarp partly detaching; columella 3–5 mm long. *Seeds* 5.2–6.2 mm diam, dark brownish when dry, sometimes marbled, hilum oblong to orbicular, 0.6–1.2 by 0.3–0.9 mm.

Distribution — Cambodia, Laos, Vietnam.

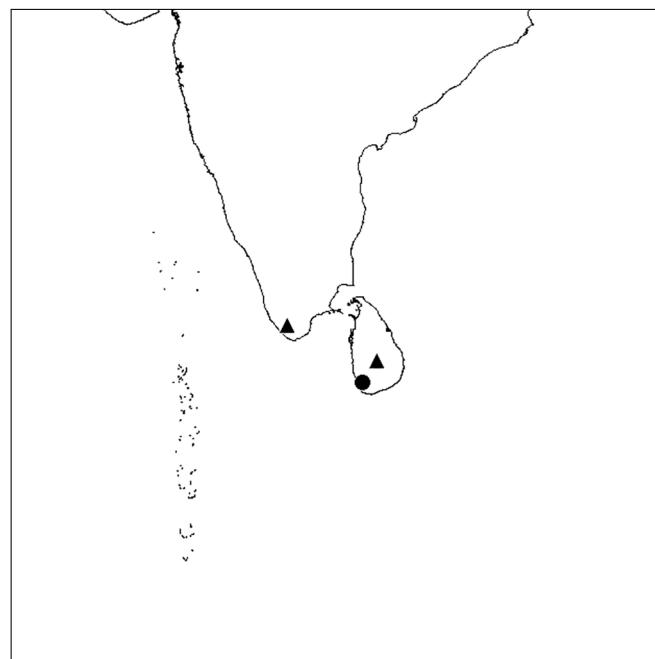
Habitat & Ecology — Shaded understory in mixed evergreen, deciduous, seasonal or degraded hardwood forests. Growing on shale bedrocks. Elevation: c. 60 m. Flowering: March, July, September to October; fruiting: July, October.

Notes — 1. The species can be recognised by its distinctly triplinerved venation.

2. An illustration attached to one of the two syntypes of *T. capitellatus* (Pierre 472, P, barcode P00717093) clearly shows a disc of 5 separate lobes in the pistillate flowers, while the other syntype (Pierre 1323, P, barcode P00717090) and our own observations indicate otherwise: the disc in the pistillate flowers is annular but often with an undulate margin.



Map 4 Distribution of *Trigonostemon cherrieri* Veillon (■) and *T. inopinatus* Airy Shaw (▲).



Map 5 Distribution of *Trigonostemon diplopetalus* Thwaites (●) and *T. nemoralis* Thwaites (▲).

6. *Trigonostemon cherrieri* Veillon — sect. *Tylosepalum* — Map 4

Trigonostemon cherrieri Veillon (1992) 55. — Type: Veillon 7385 (holo P, barcode P00057693; iso K, barcode K000959366, L, barcode L0016479, P, barcodes P00057694, P00057695, P00057696, MO*, barcode MO260396, NOU*, barcodes NOU005872, NOU005874), New Caledonia, Poya, south of Mepouiri, not far from the coast.

Shrubs, 2–4 m tall; flowering branches 0.8–3.5 mm diam, pubescent when young, glabrous in old parts. Outer bark 0.1–0.2 mm thick, pale brown to grey; inner bark 0.1–0.2 mm thick, reddish brown; wood pale yellowish. Stipules subulate, 0.15–0.3 mm long, caducous, often indistinct, pubescent at base. Leaves: petiole terete, grooved above, 0.5–2.2 cm long, 0.7–1.4 mm diam, sparsely pubescent or glabrous; blade elliptic, 3.5–11.5 by 1.8–4.9 cm, coriaceous, base acute to rounded, 2 adaxial glands present, margin entire, apex rounded, occasionally with a short notch, both surfaces glabrescent; venation pinnate, midrib flat above and elevated beneath, base slightly pubescent beneath when young, secondary veins 4–8 pairs, curved and connected along margin, tertiary veins reticulate, often obscure. Inflorescences bisexual or unisexual, terminal or axillary or cauliflorous, fascicled cymes or racemose thyrses; axis terete, up to 5.5 cm long, 0.5–1.1 mm diam, slightly pubescent, 1–2 pistillate flowers at apex, staminate flowers below; bracts lanceolate, 0.5–2.4 by 0.15–0.5 mm, pubescent outside. Staminate flowers 4.2–5.3 mm diam; pedicel 3.8–7.4 mm long, 0.3–0.5 mm diam, slightly pubescent; sepals elliptic to lanceolate, 1.2–2.1 by 0.3–1.2 mm, base connate, margin entire, apex acute to rounded, pubescent outside; petals obovate, 2–3.2 by 1.3–1.7 mm, yellow, glabrous; disc lobes semi-orbicular, c. 0.2 by 0.4 mm diam, apex rounded; stamens 3, androphore c. 1.6 mm long, c. 0.15 mm diam, anthers ellipsoid, 0.5–0.7 mm long. Pistillate flowers (fruiting) c. 2.5 mm diam; pedicel 1.1–1.7 cm long, 0.7–0.8 mm diam, glabrescent; sepals lanceolate to elliptic, 1.5–2.5 by 0.7–1.5 mm, margin entire, apex rounded to acute to sometimes acuminate; petals elliptic, 4–4.3 by 0.7–1 mm, yellow; disc not seen; ovary c. 1.1 mm diam, glabrous, style 0.3–0.5 mm long, stigmas 0.6–1 mm long, apically shortly bifid, free arms 0.15–0.4 mm long. Fruits 0.95–1.2 cm diam, glabrous; pedicel 1.8–3.4 cm long.

1.7–2 mm diam; sepals persistent but not much accrescent; wall 0.5–0.6 mm thick, exocarp partly detaching; columella 6.5–8.7 mm long. Seeds 6–7.5 mm diam, reddish brown; hilum rhombic, 1–2 by 0.5–0.6 mm.

Distribution — New Caledonia (endemic).

Habitat & Ecology — Undergrowth, on black clay. Elevation: c. 10 m. Flowering and fruiting: June and December.

Note — The species is characterised by its relatively small (up to 11.5 by 4.9 cm), coriaceous, elliptic leaves and fascicled short inflorescences.

7. *Trigonostemon diplopetalus* Thwaites — sect. *Pycnanthera* — Map 5

Trigonostemon diplopetalus Thwaites (1861) 277; Müll.Arg. (1866) 1108; Hook.f., (1887) 398; Trimen (1898) 51, pl. 83; Pax & K.Hoffm. (1911) 93, f. 39; N.P.Balakr. & Chakrab. (1991) 613, f. 3; Philcox (1997) 110. — Lectotype (designated here): Thwaites CP 578 (G*, barcode G00435106; iso A, barcode A00048867, BR*, barcode BR000005105045, CAL, barcodes CAL0000023676, CAL0000023677, FR*, barcode FR0036073, G*, no barcode, in the same folder with lectotype; G-DC*, barcode G00319791, on 2 sheets, GH*, barcode GH00048868, K, barcode K000246865, P, barcodes P00717097, P00717098), Sri Lanka.

Shrubs or small trees; flowering branches 2–2.8 mm thick, pubescent when young, glabrous in older parts. Outer bark 0.1–0.2 mm diam, dark to pale brown; inner bark 0.1–0.3 mm thick; wood pale yellow. Stipules subulate, 0.4–1 mm long, caducous, pubescent at base. Leaves: petiole terete but grooved above, 0.5–1.2 cm long, 1–1.7 mm diam, slightly pubescent when young; blade oblong to oblanceolate, 14–23.5 by 3.5–5.5 cm, thick chartaceous, lower part cuneately narrowed, decurrent into petiole, 2 adaxial glands present, falcate, margin distantly serrate, teeth falcate, apex acuminate, both surfaces glabrous, slightly pubescent beneath when young; venation pinnate, midrib almost flat above, elevated beneath, secondary veins 11–16 pairs, bifurcate and connected along margin, tertiary veins reticulate, obscure. Inflorescences bisexual, racemose thyrses, terminal; axis 3.3–17 cm long, 1.2–1.7 mm diam, pubescent; bracts lanceolate, 0.2–1.3 by 0.4–0.7 mm, pubescent. Staminate flowers (bud) 2–2.2 mm diam; pedicel 1.1–2.5 mm long,

0.35–0.4 mm diam, pubescent; sepals lanceolate, 1.3–1.5 by 0.5–0.7 mm, base connate, apex rounded to acute, pubescent outside; petals (Trimen 1898) about as long as sepals, denticulate and crisped, bilobed, red; disc glands 5 (Balakrishnan & Chakrabarty 1991), c. 0.2 by 0.3 mm; stamens (Balakrishnan & Chakrabarty 1991) 3, sessile? (see note 2), connective fleshy, forming a stalk, c. 0.5 mm long. *Pistillate flowers* (bud) 2–2.1 mm diam; pedicel 5.2–6 mm long, apically 0.5–0.7 mm diam, pubescent; sepals lanceolate to oblong, 2–2.6 by 0.7–1 mm, apex acuminate, pubescent and gibbose (with a horn-like appendage) outside (Balakrishnan & Chakrabarty 1991); petals (Trimen 1898) as in staminate flowers, but larger and reflexed; ovary (Philcox 1997) pubescent, stigmas (Trimen 1898) apically twice bifid, with short stout branches. *Fruits* (Philcox 1997) 1–1.5 cm diam, subglobose. *Seeds* (Philcox 1997) 5.5–6 mm diam, pale brown, with shallow longitudinal ridge.

Distribution — Sri Lanka (endemic).

Habitat & Ecology (Trimen 1898) — Forests in moist regions. Elevation: 0–300 m. Flowering: March to May, September.

Notes — 1. A very rare species, endemic to Sri Lanka. It is possibly allied to *T. nemoralis* Thwaites because of the sessile anthers. The petals are bilobed.

2. In Balakrishnan & Chakrabarty's revision (1991), the anthers are said to be sessile in the text, but the illustration shows a filament below, supporting the anthers.

8. *Trigonostemon eberhardtii* Gagnep. — sect. *Tylosepalum* — Fig. 1; Map 6

Trigonostemon eberhardtii Gagnep. (1922) 749; (1925b) 313. — Lectotype (designated here): Bon 5239 (P, barcode P00717103), Vietnam, Annam, Thanh-hoa. — Other syntypes: Eberhardt 4293 (P, barcodes P00717101, P00717102), Vietnam, Tonkin, Hoa-binh, Mai-ha; Bon 5465 (P, barcodes P00717099, P00717100), Vietnam, Annam, Son-thôn.

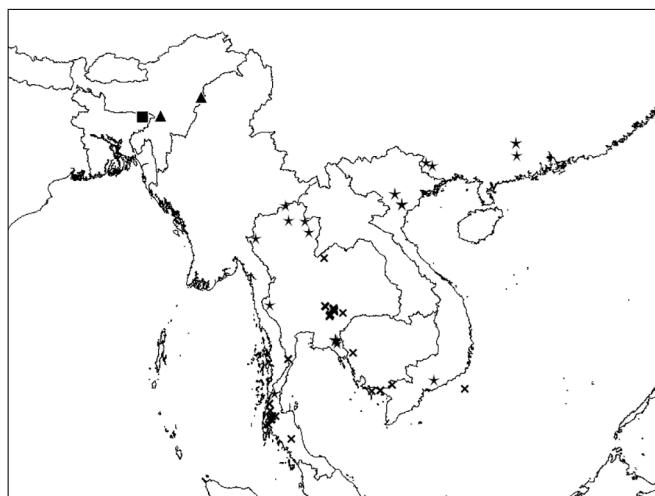
Trigonostemon harmandii Gagnep. (1922) 750; (1925b) 313. — Type: Harmand 2956 (P, barcodes P00648665, P00648666, P00648667), Cambodia. *Trigonostemon poilanei* Gagnep. (1922) 753; (1925b) 314. — Type: Poilane 40807 (A, barcode A00048878, P, barcode P00717127), Vietnam, Bien-hoa, Giaray.

Trigonostemon albiflorus Airy Shaw (1971) 547; (1972) 345; Chantar. (2005) 23; (2007) 574, f. 92; P.T.Li & M.G.Gilbert (2008) 273. — *Trigonostemon leucanthus* Airy Shaw var. *siamensis* H.S.Kiu in Kiu & Chen (1992) 211. — Type: Winit 1704 (holo K, on 2 sheets, barcodes K000959303, K000959304; iso BK, barcode BK257891, BM, barcode BM000951503), Thailand, Lampang, Mê Pêng.

Trigonostemon leucanthus Airy Shaw (1971) 548; H.S.Kiu (1996) 164. — Type: Morse 668 (K, barcodes K000959336, K000959337), China, Guangxi, Longzhou.

Trigonostemon wui H.S.Kiu (1995) 19, f. 2. — Type: Kiu [H.X. Qiu] 451 (holo IBSC, not found; iso BK, barcode IBK00190788), China, Guangdong, Fengkai, Yulao.

Shrubs or small trees, 1–5(–7) m tall, dbh 2.8–6.3 cm; flowering branches 1.1–5 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts (and sometimes petals). *Outer bark* c. 0.1 mm thick, dark to pale brown or greyish brown; *inner bark* 0.1–0.2 mm thick, brown to reddish brown; wood white to pale yellowish. *Stipules* subulate, 0.3–0.7 mm long, caducous, often pubescent. *Leaves*: petiole terete, grooved or flat above, 0.5–8 cm long, 0.7–2.1 mm diam, glabrous or pubescent; blade elliptic, 8.5–26 by 2.5–8 cm, chartaceous, base acute, 2 adaxial glands present, occasionally sparsely pubescent, margin entire or very distantly serrate, apex acuminate to caudate, upper surface glabrous, dark green, lower surface often very sparsely pubescent, pale green; venation triplinerved, midrib (and sometimes 2 basal secondary veins) slightly raised above and distinctively elevated beneath, pubescent on lower surface, especially near base, other secondary veins 4–7(–10) pairs, bow-shaped and connected along margin, tertiary veins



Map 6 Distribution of *Trigonostemon eberhardtii* Gagnep. (★), *T. montanus* R.Y.Yu & Welzen (▲), *T. praeteritus* Airy Shaw (■) and *T. quocensis* Gagnep. (×).

scalariform, veinlets reticulate. *Inflorescences* bisexual, terminal or axillary, paniculate, pistillate flowers open before staminate ones; main axis terete, up to 31.5 cm long, 0.4–2.7 mm diam, pubescent to glabrous; bracts linear to lanceolate to triangular, 0.7–2.7 by 0.3–0.6 mm, pubescent outside; bracteoles linear to lanceolate, 0.4–0.7 by 0.1–0.2 mm, densely pubescent. *Staminate flowers* 6–8 mm diam; buds conical; pedicel 2–9.5 mm long, 0.15–0.3 mm diam, glabrous, light green; sepals elliptic, 1–2.3 by 0.5–0.7 mm, light green, base connate, margin entire, apex acute, often with a short notch and an adaxial gland, pubescent outside; petals obovate, 2.8–5 by 1.5–3 mm, contort, membranous, white, lower part cuneately narrowed, apex rounded, glabrous; disc annular, yellow, margin undulate, often deeply notched, 0.4 (inner margin)–0.6 mm (outer margin) diam; stamens 3, androphore 0.9–1.2 mm long, 0.1–0.2 mm diam, white, free part of filaments c. 0.2 mm long, white, anthers free, globose to ellipsoid, 0.3–0.4 mm long, yellow. *Pistillate flowers* 6–9 mm diam; buds conical; pedicel slightly thickening toward apex, 3–15.5 mm long, apically 0.45–1.1 mm diam when flowering, glabrescent; sepals as staminate flowers but larger, 1.3–3.8 by 0.6–1.3 mm, apex often with an adaxial gland but without notch; petals as staminate flowers; disc lobes 5, rectangular, 0.3–0.45 by 0.3–0.4 mm, yellow, apex truncate; ovary 1–1.1 mm diam, glabrous, green, style 0.1–0.2 mm long, stigmas 0.8–1.1 mm long, bent, white, apically slightly thickened and slightly bifid. *Fruits* 1.1–1.5 cm diam, greenish, glabrous; pedicel 1.9–3.4 cm long, 1.2–1.8 mm diam; sepals persistent but not accrescent; wall 0.4–0.5 mm thick, exocarp partly detaching; columella 4.5–6.5 mm long. *Seeds* 7–8 mm diam, marbled; hilum rhombic, 2.5–3 by 1–2 mm.

Distribution — China, Thailand, Laos, Cambodia, Vietnam.

Habitat & Ecology — Evergreen or deciduous forests, growing on limestone, sometimes in shaded areas near rivers. Elevation: 150–1300 m. Flowering: March to December; fruiting: May to December.

Notes — 1. *Trigonostemon eberhardtii* is characterised by the translucent (oil?) dots and white petals (the label of a specimen from Thailand, Sangkhachand 531, indicates that the petals are yellow, but this is a very exceptional case and the label could be wrong). Although the dots are not always present in all green parts (young branches, petiole, leaf blade, inflorescences, sepals, ovary and fruits), when present, it is a good spotting character, particularly in herbarium material.

2. The species resembles *T. viridissimus*, with which the morphological boundary is sometimes unclear. However, the



Fig. 1 *Trigonostemon eberhardtii* Gagnep., private collection of Hua-Shing Kiu, originally from Yulao, Fengkai, Guangdong, China. a. Growing habit; b. leaf base, showing glands; c. top view of staminate flower; d. lateral view of flower buds and staminate flower; e. pistillate flower; f. fruit; g. inflorescence; h. infructescence. — Photos by Ren-Yong Yu.

molecular phylogeny (Yu et al. 2019) shows that the two species are placed in different subclades within sect. *Tylosepalum*. Main characters that can be used in identification include: 1) the white petals (yellow to orange in *T. viridissimus*); 2) monopodial branching in the inflorescences with relatively more condensed staminate flowers (vs sympodial branching and relatively loose panicles in *T. viridissimus* var. *viridissimus*); and 3) an indistinctive style (shorter than 2 mm in *T. eberhardtii*; up to 6 mm in *T. viridissimus*).

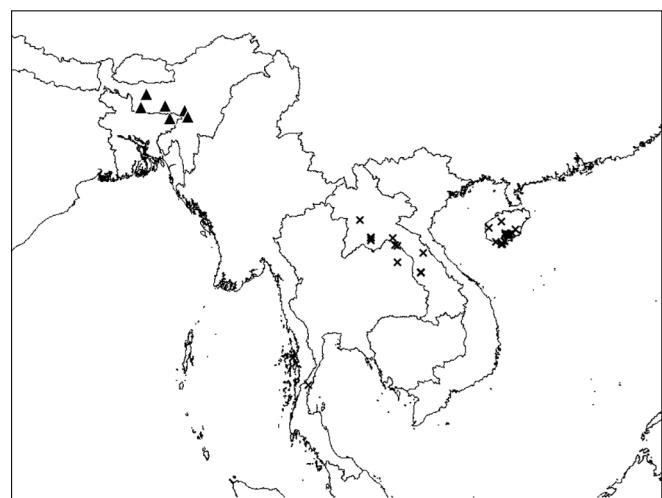
9. *Trigonostemon flavidus* Gagnep. — sect. *Trigonostemon* — Fig. 2; Map 7

Trigonostemon flavidus Gagnep. (1922) 749; (1925b) 320; P.T.Li et al. (2006) 119; P.T.Li & M.G.Gilbert (2008) 273; R.Y.Yu & Welzen (2018) 195. — Lectotype (designated here): *Harmand* 3273 (P, barcode P00717104; iso P, barcode P00717105), Laos, in Lakhon mountains, near Me-Kong.

Trigonostemon heterophyllus Merr. (1930) 38; N.P.Balakr. & Chakrab. (1991) 617, f. 5; H.S.Kiu (1996) 163; Chantar. (2005) 24; (2007) 577, pl. 31, 1. — Type: *Tsang* 594 [17343] (A*, barcodes A00048861, A00048862, B*, barcode B10 0249526, BM, barcode BM000951501, BO, sheet no. BO1695956, CAL, barcode CAL0000023662, ECON*, barcode ECON00254237, G, barcode G00435104, K, barcode K000959339, L, barcode L0160156, MO*, barcode MO-260398, NTUF*, NY*, barcode NY00273341, P, barcode P00717108, PE, barcodes PE00022683, PE00022684, UC*, barcode UC373861, US*, barcodes US00096533, US00997745, W*, sheet no. W1940-0006789, WIS*, barcode WISv0255641), China, Hainan, Taam Chau District [= Danzhou County], Sha Po Shan [= Mt Sha Bao].

Trigonostemon sunirmalii Chakrab. & N.P.Balakr. (1984b) 179. — Type: *Biswas* 22 (holo CAL, barcode CAL0000023663; iso CAL, barcode CAL0000023664), Myanmar, Tenasserim [= Tanintharyi Region], Nima-chuang.

Small trees, 1–2.5 m tall; flowering branches up to 4.5 mm diam, densely pubescent. Outer bark 0.1–0.2 mm thick, pale brown to dark grey, smooth or roughened; inner bark 0.1–0.2 mm thick, reddish brown; wood pale yellow. Stipules subulate, 0.7–1 mm long, pubescent at base. Leaves: petiole terete but sometimes flattened or grooved above, 0.2–1.2 cm long, 0.7–2.4 mm diam, densely pubescent; blade obovate or oblanceolate, cuneately narrowed and sometimes unequal in the lower middle part, 9–35 by 5–9 cm, chartaceous, base abruptly rounded to truncate, with 2 adaxial glands, margin distantly serrate, teeth small and nipple-like, apex caudate to acuminate, upper surface dark to light green, lower surface paler, both surfaces pubescent, especially on secondary veins and margin; venation pinnate; midrib thin, elevated on both surfaces, secondary veins 10–13 pairs, tertiary veins reticulate, often obscure. Inflorescences bisexual, in short cymes or thyrses, cauliflorous or supported by a peduncle and involucral bracts; peduncle 1–9 cm long, pubescent; involucral bracts lanceolate, 8–38 by 0.7–9 mm, pubescent; bracts lanceolate to linear, 1.1–5.5(–15) by 0.2–0.7(–2) mm, pubescent. Staminate flowers 3.6–6 mm diam; pedicel 2.4–4.7 mm long, 0.15–0.3 mm thick, pink to light green, glabrous; sepals elliptic or obovate, 1.1–2.4 by 0.5–1.8 mm, green, base connate, margin ciliate, apex often acute to rounded, occasionally with a notch, pubescent outside; petals obovate, 2.1–4.2 by 1.7–2.2 mm, base claw-like, apex rounded, glabrous, dark reddish to maroon-purple to black; disc lobes obovate or rectangular, 0.4–0.7 by 0.15–0.25 mm, sometimes narrowed at base, often reflected at apex, light orange, glabrous; stamens 3, androphore 1–1.2 mm long, c. 0.1 mm diam, white, shortly trifid at apex, free part of filaments 0.1–0.2 mm long; anthers free, divaricate at apex, thecae 0.4–0.6 mm long, pale yellow, connective pinkish red, with numerous droplets with secretion. Pistillate flowers few, slightly enlarged when fruiting, up to c. 1 cm diam; pedicel c. 1.5 mm long and c. 0.5 mm diam in flower bud, accrescent to c. 7 mm long and apically c. 1 mm diam when fruiting; sepals lanceolate to linear, 2.2–3.4 by 1–1.5 mm when flowering, accrescent to 2.4 by 0.9 cm in fruit, margin



Map 7 Distribution of *Trigonostemon flavidus* Gagnep. (x) and *T. semperflorens* (Roxb.) Müll.Arg. (▲).

entire or with a few teeth, apex acuminate, pubescent outside; petals elliptic, 3–3.3 by 2–2.7 mm (flower bud), caducous; disc glands rectangular to semi-orbicular, 0.5–0.6 by 0.4–0.6 mm, rounded or truncate at apex, glabrous; ovary c. 0.7 mm diam, bright dark green, densely pubescent, style almost indistinct, stigmas 3, completely divided, free arms 0.6–0.7 mm long. Fruits c. 1.2 cm diam, green when young, brown when mature, densely pubescent; wall woody, 0.5–0.55 mm thick; columella 4.2–6.7 mm long. Seeds 4.2–6.7 by 4.5–5.7 mm, light or dark brownish when dry, hilum irregularly shaped, more or less triangular, 0.8–1.3 by 0.5–0.7 mm diam.

Distribution — Myanmar (Tenasserim), China, Laos, Thailand, Malay Peninsula.

Habitat & Ecology — Understorey in evergreen forests to deciduous hardwood or bamboo forests, often near rivers, growing on sandstones to conglomerate bedrocks. Elevation: c. 200 m. Flowering: January to March, July; fruiting: February, July to October.

Note — *Trigonostemon flavidus* strongly resembles *T. semperflorens* (Roxb.) Müll.Arg. from India but has much denser and stronger hairs (Yu & Van Welzen 2018, Balakrishnan & Chakrabarty 1991). We treat them as separate species, because there is a clear gap in the extent of pubescence (pubescent in *T. flavidus* but glabrous in *T. semperflorens*; no intermediate forms are found) and there is a gap in the distribution – both species are absent in central Myanmar (*T. flavidus* has its western most limit in S Myanmar (Tenasserim) and *T. semperflorens* occurs in NE India and Bangladesh).

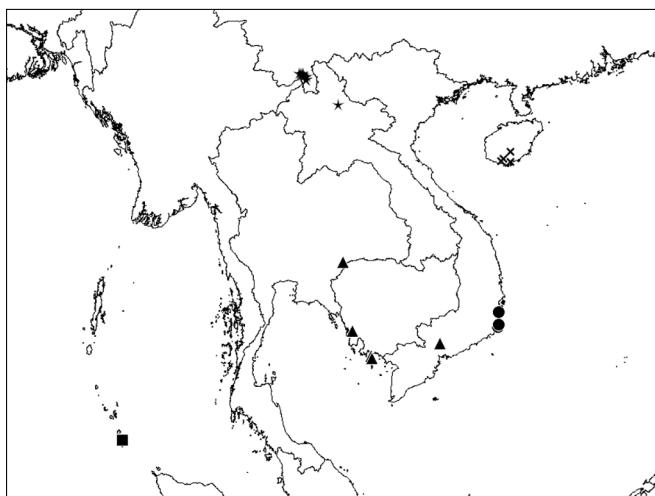
10. *Trigonostemon fragilis* (Gagnep.) Airy Shaw — sect. *Tylosepalum* — Map 8

Trigonostemon fragilis (Gagnep.) Airy Shaw (1978) 415. — *Poilaniella fragilis* Gagnep. (1925a) 467; (1925b) 307; P.T.Li et al. (2006) 119; P.T.Li & M.G.Gilbert (2008) 274. — Lectotype (designated here): *Poilane* 2927 (P, barcode P00712172; iso A*, barcode A00106974, P, barcodes P00712173, P00712174), Vietnam, Annam, Tre Island, near Nhatrang.

Shrubs, 2–3 m tall; flowering branches 1.1–2.5 mm diam, pubescent when young, glabrous in old parts. Outer bark 0.1–0.2 mm thick, pale brown to grey; inner bark 0.1–0.3 mm thick, pale to reddish brown; wood pale yellowish to brown. Stipules subulate, 0.2–0.5 mm long, caducous, often indistinct, pubescent at base. Leaves: petiole terete, grooved above, 0.5–2.4 cm long, 0.5–1 mm diam, glabrescent; blade elliptic to ovate, 1.8–5.5 by 1.2–3 cm, chartaceous, base acute to rounded or sometimes truncate, 2 adaxial glands present, margin entire,



Fig. 2 *Trigonostemon flavidus* Gagnep., cultivated in South China Botanical Garden. a. Growing habit; b. bark; c. cauliflorous staminate inflorescences; d. lateral view of staminate flower; e. top view of staminate flower; f. back view of staminate flower; g. young pistillate flowers and mature fruit; h. young fruit; i. staminate flower with 4 stamens (abnormal growth). — Photos by Ren-Yong Yu.



Map 8 Distribution of *Trigonostemon fragilis* (Gagnep.) Airy Shaw (●), *T. ili* Y.T.Chang (★), *T. murtonii* Craib (▲), *T. villosus* Hook.f. var. *nicobaricus* (Chakrab.) N.P. Balakr. & Chakrab. (■) and *T. xyphophyloides* (Croizat) L.K.Dai & T.L.Wu (✗).

apex acute or rounded, both surfaces glabrescent, particularly pubescent within the axils of midrib and lateral veins and one or more domatia sometimes present; venation triplinerved, midrib and basal secondary veins flat or slightly raised above and elevated beneath, other secondary veins 3–4 pairs, curved and connected along margin, tertiary veins reticulate, often obscure. Inflorescences seemingly unisexual, terminal or axillary, cymes or thyrses; axis terete, 1–3.8 cm long, 0.4–0.7 mm diam, glabrescent; bracts lanceolate to oblong, 0.2–1 by 0.2–0.5 mm, pubescent outside. Staminate flowers (bud) c. 2.4 mm diam; pedicel 6.4–7.5 mm long, slightly thickening toward apex, 0.3–0.7 mm diam, slightly pubescent; sepals elliptic, unequal, 1.2–2.1 by 0.9–1.5 mm, margin entire, apex rounded, pubescent outside; petals flabellate, but elliptic when young, 1.5–1.6 by 1–1.4 mm, apex sometimes slightly bilobed; disc annular, c. 0.2 mm wide; stamens 3, androphore erect, c. 0.1 mm long, anthers ellipsoid, 0.8–0.9 mm long. Pistillate flowers (flattened) c. 1 cm diam; pedicel slightly thickening toward apex, 7.3–10 mm long, apically 0.5–0.7 mm diam; sepals elliptic, 1.6–3.2 by 0.9–1.4 mm, margin entire, apex acute, pubescent outside; petals flabellate, 3.2–5 by 3.2–5.4 mm, apex slightly bilobed; disc annular, 0.2–0.3 mm wide; ovary 0.7–1 mm diam, glabrous, style absent, stigmas 0.4–0.55 mm long, thickened and with a very shallow groove at apex. Fruits 1.2–1.3 cm diam, glabrous; wall 0.7–1 mm thick, exocarp 0.3–0.6 mm thick, completely detached; columella 7.1–7.8 mm long. Seeds flattened globose, 10–10.5 by 9–9.5 mm, hilum oblong, 2.3–2.4 by 1.1–1.5 mm.

Distribution — China (Hainan?), Vietnam (Ninh Hai District, Ninh Thuan Province).

Habitat & Ecology — In forests, dry and level lands, or near salt fields or lakes; on sandy soil or clay. Flowering: April; fruiting: January, April.

Note — This is the only species in *Trigonostemon* with domatia in some leaves.

11. *Trigonostemon heteranthus* Wight — sect. *Tylosepalum* — Map 1

Trigonostemon heteranthus Wight (1852) 24, t. 1890; Müll.Arg. (1866) 1109; Kurz (1877b) 406 ('*heteranthum*'); Hook.f. (1887) 396; N.P.Balakr. & Chakrab. (1991) 615, f. 4. — Lectotype (designated here): Griffith KD 4796 (K, barcode K000246910; iso P, barcode P00717107), Myanmar, Mergui. — Other syntypes: Griffith s.n. (K, barcode K000246861), Myanmar, Mergui; Helfer KD 4796 (K, barcode K000246862), Myanmar, Mergui.

Shrubs, 1.3–5 m tall, dbh c. 6.4 cm; flowering branches 2.3–3 mm diam, often pubescent when young. Outer bark 0.1–0.2 mm thick, pale brown to slightly reddish brown; inner bark 0.1–0.2 mm thick, dark reddish brown; wood pale yellow. Stipules subulate, 0.9–1.8 mm long, pubescent at base. Leaves: petiole terete but grooved above, 1–15.8 cm long, thickened at apex and base, in middle 0.7–1.9 mm diam, slightly pubescent when young; blade elliptic to oblong or oblanceolate, 7.8–28 by 2.6–10 cm, chartaceous, base rounded to acute to acuminate, with 2 adaxial glands, margin distantly serrate, teeth glandular or falcate, apex acuminate to slightly caudate, both surfaces glabrous, but pubescent beneath when young; venation pinnate; midrib slightly elevated above and distinctively elevated beneath, sometimes sparsely pubescent beneath, secondary veins 9–17 pairs, bifurcate and connected along margin, veinlets reticulate, often obscure. Inflorescences bisexual or unisexual, racemosous thyrses, often terminal, pistillate flowers single per node, open first; axis 4–21 cm long, 0.6–1.4 mm diam, pubescent; involucral bracts as stipules, but somewhat longer, 1.1–2.4 mm long; bracts under each node and flower, lanceolate, 0.6–4.1 by 0.2–1 mm. Staminate flowers c. 2 mm diam; pedicel 4.5–7.5 mm long (2–5 mm long below articulation, c. 5 mm long above articulation), 0.1–0.2 mm diam, glabrous; sepals elliptic, 1–1.6 by 0.8–1.1 mm, base connate, margin serrate, apex acute to rounded, pubescent; petals elliptic to obovate, c. 2.5 by 2 mm, white; disc glands 5; stamens 3, clustered on an erect androphore. Pistillate flowers 5–7.3 mm diam; pedicel 8–11.5 mm long and apically 0.4–0.6 mm diam when flowering, elongating to 1.9–2.6 cm long and apically 0.8–1.2 mm diam when fruiting, an articulation present at 2/3 of length below apex; sepals ovate to triangular, 1.8–2.5 by 0.8–1.5 mm when flowering, accrescent to 5.2–7 by 2–3 mm when fruiting, base connate, margin fringed and serrate, with capitate glands; petals obovate, 2.4–3.4 by 1.4–2.4 mm, contort and conical in bud, white; disc lobes semi-orbicular, c. 0.2 by 0.6 mm, apex rounded, glabrous; ovary 0.8–1.2 mm diam, glabrous, style 0.15–0.2 mm long, stigmas 0.5–0.6 mm long, thickened but not bifid at apex. Fruits c. 1 cm diam. Seeds not seen.

Distribution — Myanmar (Mergui and Tavoy, endemic).

Habitat & Ecology — In forests. Elevation: 65–200 m. Flowering: January to March.

Note — The species is similar to *T. kerrii* Craib in the fringed pistillate sepals with capitate glands, but differs in the white petals and the stigmas without division.

12. *Trigonostemon inopinatus* Airy Shaw — sect. *Spinipollen* — Map 4

Trigonostemon inopinatus Airy Shaw (1976) 396; (1980) 691. — Type: Webb & Tracey 7762 (holo BRI, barcode BRI-AQ0205473, on 2 sheets), Australia, Queensland, Cawley State Forest, west of Cathu between Mackay & Proserpine.

Small trees or shrubs, up to 7 m tall; flowering branches 1.1–2.2 mm diam, pubescent when young, glabrous in old parts. Outer bark c. 0.1 mm thick, pale brown to grey; inner bark c. 0.1 mm thick, reddish brown; wood pale yellowish. Stipules subulate, 0.1–0.35 mm long, sometimes pubescent at base. Leaves: petiole terete, grooved above, 1–2.2 cm long, 0.8–1.7 mm diam, sometimes very slightly thickened towards base and apex, pubescent; blade elliptic, 5–10 by 2.4–4.8 cm, chartaceous, base acute, 2 adaxial glands present, margin distantly serrate, apex acute to acuminate, upper surface pubescent when young, glabrescent, lower surface often pubescent; venation pinnate, midrib flat above and elevated beneath, pubescent beneath, secondary veins 4–8 pairs, curved and connected along margin, tertiary veins reticulate, often obscure. Inflorescences

bisexual, axillary; staminate ones thyrsoid, dichotomously branching, often subtended by bracts and supported by a peduncle, peduncle terete, 0.8–4.5 cm long, 0.4–1 mm diam, pubescent, bracts oblong, 2.8–25 by 1–6 mm, pubescent on both sides; pistillate inflorescences cymes, peduncle terete, 1.2–2.5 cm long, 0.5–1 mm diam, bracts oblong to lanceolate, 7–16 by 2–3.8 mm, pubescent on both sides. *Staminate flowers* c. 6 mm diam; pedicel thickening toward apex, 4.2–6 mm long, apically 0.4–0.6 mm diam, pubescent; sepals elliptic to lanceolate, 1.8–2.7 by 0.7–0.8 mm, base connate, margin entire, apex acuminate, pubescent outside; petals obovate to flabellate, 3–3.5 by 2.1–2.2 mm, yellow or cream, glabrous, with a reddish honey mark near base, apex rounded; disc glands 5, 0.5–0.6 by 0.2–0.3 mm; stamens 3, androphore c. 1.3 mm long, c. 0.4 mm diam, anthers ellipsoid, 0.7–0.8 mm long. *Pistillate flowers* c. 7.5 mm diam; pedicel thickening toward apex, 9.5–13 mm long and apically 1–1.2 mm diam when flowering, elongating to 1.7–2.3 cm long and apically 1.5–1.7 mm diam in fruit, pubescent; sepals lanceolate, 4–7.5 by 1.2–2.2 mm when flowering, enlarged up to 18 by 6.7 mm when fruiting, green, pubescent on both sides, base connate, margin entire, apex acuminate; petals as in staminate flowers, but larger and caducous, 4–5 by 3.5–4.8 mm; disc annular, 5-notched, membranous; ovary c. 1.6 mm diam, pubescent; style absent; stigmas 0.9–1 mm long, in middle c. 0.5 mm diam, adaxially grooved, apically thickened and horseshoe-like, 0.8–0.9 mm diam. *Fruits* sparsely pubescent; sepals persistent; wall 0.4–0.5 mm thick, exocarp partly detaching; columella 5.5–6.5 mm long. *Seeds* 6.7–7 mm diam, brown; hilum round, 1.7–1.8 by 1–1.5 mm.

Distribution — Australia (Queensland, endemic).

Habitat & Ecology — Notophyll Vine forests, on granite, near streams. Elevation: 140–820 m. Flowering: May to July; fruiting: February and July.

Note — See note under *T. montanus* R.Y.Yu & Welzen. The short and dichotomously branching staminate inflorescences are typical for the species.

13. *Trigonostemon kerrii* Craib — sect. *Trigonostemon* — Map 1

Trigonostemon kerrii Craib (1924) 97; Gagnep. (1925b) 321; Airy Shaw (1972) 346; Chantar. (2005) 25; (2007) 577. — Lectotype (designated by Chantaranothai 2005): Kerr 5871 (BK*, barcode BK239811; iso A*, barcode A00048870, P, barcode P04810877), Thailand, Nakawn Tai.

Shrubs or small trees, 2–3 m tall; flowering branches 1.5–2.8 mm diam, pubescent when young, glabrous in old parts. Outer bark 0.1–0.2 mm thick, pale grey to brown; inner bark c. 0.1 mm thick, dark reddish; wood pale yellowish to white. *Stipules* subulate, 0.5–1 mm long, caducous, pubescent at base. *Leaves*: petiole terete but grooved above, 0.7–2.8 cm long, 0.9–1.2 mm diam, slightly pubescent; blade oblong to oblanceolate, 10.5–21 by 1.8–4.4 cm, chartaceous, base acute, with 1–2 pairs of adaxial glands, margin distantly serrate, teeth glandular, apex acuminate, upper surface glabrous, lower surface glabrescent; venation pinnate, midrib slightly raised above and elevated beneath, slightly pubescent beneath, secondary veins 8–11(–16) pairs, curved and connected along margin, tertiary veins reticulate, often obscure. *Inflorescences* seemingly unisexual, subterminal; staminate ones racemose thyrses, pistillate ones racemes; axis 1–11.2 cm long, 0.4–0.75 mm diam, pubescent; bracts lanceolate, 0.5–3.6 by 0.2–0.9 mm, pubescent. *Staminate flowers* c. 2.8 mm diam; pedicel 2.5–6 mm long, 0.1–0.2 mm diam, glabrescent; sepals elliptic to lanceolate, 0.9–1.5 by 0.5–0.9 mm, base connate, margin often serrate, apex acuminate to rounded, pubescent outside; petals in flower bud elliptic, 1.1–1.4 by 0.7–0.9 mm, apex rounded,

purplish red (Craib 1924); disc glands 5, c. 0.15 by 0.1 mm; stamens 3, androphore indistinct (flower too young), anthers ellipsoid, 0.7–0.8 mm long. *Pistillate flowers* (bud) c. 1.7 mm diam; pedicel c. 2.6 mm long, 0.4–0.5 mm diam, glabrescent; sepals triangular, 1.6–1.9 by 0.7–0.9 mm, base connate, margin fringed with capitate glands, apex acuminate; petals elliptic, 1.7–2.2 by 1–1.3 mm, apex rounded, purplish red (Craib 1924); disc glands 5, c. 0.2 by 0.2 mm; ovary c. 0.7 mm diam, glabrous, style absent, stigmas c. 0.25 mm long, apically seemingly bifid. *Fruits* glabrous; pedicel c. 1.8 cm long, c. 0.7 mm diam, glabrescent; sepals accrescent, persistent, lanceolate, 5–6 by 1.5–2 mm, margin fringed with capitate glands; wall 0.3–0.4 mm thick, exocarp not detaching; columella c. 3 mm long. *Seeds* not seen.

Distribution — Thailand, Cambodia (Kampong Thom).

Habitat & Ecology — In evergreen forests. Elevation: 100–200 m. Flowering: March; fruiting: April.

Note — The species resembles *T. heteranthus* in the pistillate sepals with a fringed margin with capitate glands, but it has a shorter petiole and shorter inflorescences, purplish red petals (vs white in *T. heteranthus*) and bifid stigmas (vs not bifid in *T. heteranthus*).

14. *Trigonostemon laevigatus* Müll.Arg. — sect. *Tylosepalum*

Trigonostemon laevigatus Müll.Arg. (1864b) 538; (1866) 1111; Boerl. (1900) 232, 284; Pax & K.Hoffm. (1911) 94; Merr. (1921) 345 (2nd mentioning, first = *Microdesmis caseariifolia* Planch., see Jablonski 1963: 168); Ridl. (1924) 265; Jabl. (1963) 167; Airy Shaw (1972) 346; Whitmore (1973) 135; Airy Shaw (1975) 203; (1978) 417; (1981) 355; (1983) 47; Chantar. (2005) 25; (2007) 578, f. 93; R.Y.Yu & Welzen (2018) 195, f. 5. — Lectotype (designated by Yu & Van Welzen 2018): Motley 686 (K, barcode K000959291), Borneo, South Kalimantan, Bangarmassing [= Banjarmasin].

Description & Taxonomic notes — See Yu & Van Welzen 2018.

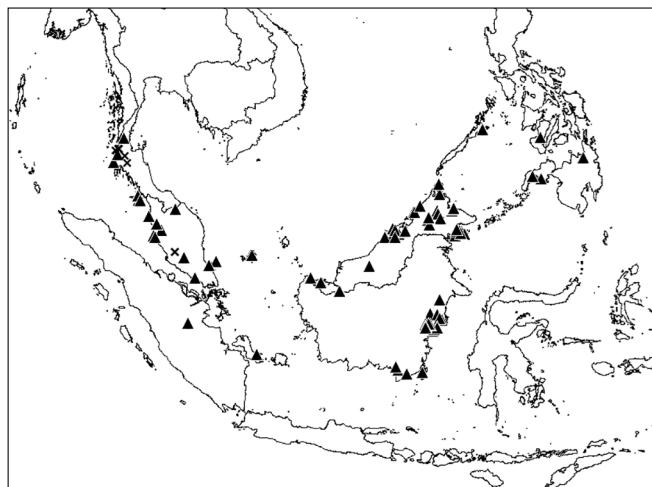
Key to the varieties

1. Sepals without a gland outside a. var. *laevigatus*
1. Sepals with a gland outside b. var. *croceus*

a. var. *laevigatus* — Map 9

Description & Taxonomic notes — See Yu & Van Welzen 2018.

Distribution — Vietnam?, Thailand, Malay Peninsula, Sumatra, Java, Borneo, Philippines.



Map 9 Distribution of *Trigonostemon laevigatus* Müll.Arg. var. *laevigatus* (▲) and *T. laevigatus* Müll.Arg. var. *croceus* (B.C.Stone) R.Y.Yu & Welzen (×).

b. var. *croceus* (B.C.Stone) R.Y.Yu & Welzen — Map 9

Trigonostemon laevigatus Müll.Arg. var. *croceus* (B.C.Stone) R.Y.Yu & Welzen (2018) 197. — *Trigonostemon croceus* B.C.Stone (1980) 249. — Type: Stone 9586 (holo KLU, sheet no. 13345; iso K, L, barcode L.2258563), Malaysia, Selangor, on the Pahang border at Genting Sempah.

Description & Taxonomic notes — See Yu & Van Welzen 2018.

Distribution — Thailand (Surat Thani, Phangnga, Ranong), Malay Peninsular (Selangor).

15. *Trigonostemon lanceolatus* (S.Moore) Pax — sect. *Trigonostemon* — Map 3

Trigonostemon lanceolatus (S.Moore) Pax in Pax & K.Hoffm. (1911) 92. — *Nepenthandra lanceolata* S.Moore (1905) 149, pl. 471, f. 7–13. — Type: *Beddome s.n.* (BM, barcode BM000951502), Myanmar, Tenasserim [= Taintharyi Region], Mooleyit slopes. *Trigonostemon phyllocaalyx* Gagnep. (1925a) 469; (1925b) 312; Airy Shaw (1972) 348; Chantar. (2005) 27; (2007) 581, syn. nov. — Type: *Poilane* 2700 (A, barcode A00048879, P, barcodes P00717119, P00717120), Vietnam, Annam, Nhatrang.

Trees, up to 5 m tall, dbh up to 5 cm; flowering branches 1.9–3.5 mm diam, pubescent when young, glabrous in old parts. Outer bark 0.1–0.2 mm thick, brown to pale or greyish brown; inner bark 0.1–0.2 mm thick, reddish brown, sap red; wood yellow to brown. Stipules subulate, 0.4–1.1 mm long, caducous, pubescent at base. Leaves: petiole terete, grooved above, 1.4–11.5 cm long, 0.8–2 mm diam, hirsute to glabrous; blade lanceolate to oblong, 6.8–21 by 2.3–8.2 cm, thick-chartaceous, base acute to rounded, 2 adaxial glands present, margin distantly serrate, apex acuminate to slightly caudate, both surfaces glabrous; venation pinnate, midrib flat or slightly raised above and elevated beneath, sometimes slightly pubescent beneath, secondary veins 6–10 pairs, curved, connected along margin, tertiary veins and veinlets reticulate. Inflorescences bisexual, often axillary, racemose thyrses, pistillate flowers open first, single per node near apex of axis, staminate flowers usually 1–3 per node below; axis up to 8.7 cm long, 0.5–0.8 mm diam, hirsute to glabrescent, bracts oblong, 0.4–6.5 by 0.1–1.4 mm, pubescent. Staminate flowers (bud) c. 2.4 mm diam; pedicel thickening toward apex, 1.8–2.5 mm long, apically 0.4–0.8 mm diam, slightly hirsute; sepals ovate to elliptic, 1.2–1.9 by 0.8–1.5 mm, base connate, margin entire, sometimes ciliate, apex rounded to acute, pubescent or hirsute outside; petals ovate to elliptic, 1.1–1.4 by 0.9–1.15 mm diam, glabrous, apex rounded; disc annular, c. 0.1 mm wide, ring c. 0.8 mm diam; stamens 3, androphore c. 0.1 mm long, anthers ellipsoid, 0.5–0.7 mm long, divaricate. Pistillate flowers 5–10 mm diam; pedicel thickening toward apex, 3–7 mm long, apically 1–1.2 mm diam, pubescent or hirsute; sepals triangular, 4–5.5 by 2.7–3 mm when flowering, significantly accrescent, up to 1.3 by 1.1 cm when fruiting, densely hirsute on both sides, base connate, margin mostly entire but with two teeth near apex, apex acuminate; petals elliptic, 2.5–3 by 1.8–2.6 mm, apex rounded; disc seemingly annular, c. 0.6 mm wide; ovary c. 1.7 mm diam, glabrous to hirsute; style absent; stigmas deeply bifid, 0.6–0.7 mm long, free arms V-shaped at base. Fruits 1–1.1 cm diam, densely hirsute, smooth; sepals persistent; wall 0.3–0.4 mm thick. Seeds c. 7.5 mm diam, marbled; hilum triangular, c. 2.5 by 1.7 mm.

Distribution — Myanmar (Tenasserim), Thailand (Chanthaburi), Vietnam (Annam).

Habitat & Ecology — Evergreen forests, on rocky or sandy soil, near stream. Flowering: December to March; fruiting: December to January.

Note — The species is characterised by the much accrescent and hirsute sepals in the pistillate flowers.

16. *Trigonostemon lii* Y.T.Chang — sect. *Tylosepalum* — Map 8

Trigonostemon lii Y.T.Chang (1983) 175; H.S.Kiu (1996) 166. — Type: Li 4576 (holo KUN, barcode KUN1294357), China, Yunnan, Xishuangbanna Botanical Garden.

Shrubs or small trees, 1–4.5 m tall; flowering branches 1.2–2.5 mm diam, pubescent when young, glabrous in old parts. Indumentum of simple hairs; translucent (oil?) dots absent in green parts. Outer bark c. 0.1 mm thick, dark brown to somewhat reddish brown; inner bark c. 0.1 mm thick, reddish brown to dark red; wood pale yellowish. Stipules subulate, 0.5–0.8 mm long, caducous, often pubescent. Leaves: petiole terete, grooved above, 0.5–2 cm long, 0.9–1.5 mm diam, slightly pubescent when young; blade oblong, 8.5–18 by 2–5.2 cm, coriaceous, base acute, 2 adaxial glands present, margin very distantly serrate, apex acuminate to somewhat caudate, upper surface glabrous, lower surface glabrescent; venation very distinctively triplinerved, midrib slightly raised above and elevated beneath, sometimes slightly pubescent beneath, secondary veins 3–7 pairs, bow-shaped (except for 2 basal secondary veins) and connected along margin, tertiary veins scalariform, veinlets reticulate, obscure. Inflorescences bisexual, terminal or axillary, paniculate thyrses, pistillate flowers single per node, staminate flowers often a cyme per node; main axis terete, 6.5–10 cm long, 0.4–1 mm diam, pubescent; bracts linear to lanceolate, 1–7 by 0.2–1 mm, pubescent. Staminate flowers 6–7 mm diam; pedicel 4–7 mm long, 0.2–0.3 mm diam, slightly pubescent; sepals elliptic to lanceolate or oblong, 1.1–2.3 by 0.7–1 mm, base connate, margin entire, apex acute to acuminate, pubescent and often with a notch and a gland outside; petals obovate, 2.8–3.5 by 1.5–2 mm, contort, membranous, yellow, apex rounded, glabrous; disc annular, margin undulate, often deeply notched, c. 0.4 mm wide; stamens 3, androphore c. 0.9 mm long, c. 0.2 mm diam, free part of filaments 0.1–0.2 mm long, white, anthers free, ellipsoid, 0.5–0.6 mm long. Pistillate flowers 7–13 mm diam; pedicel slightly thickening toward apex, 0.8–1.7 cm long, 0.7–1.1 mm diam, slightly pubescent; sepals lanceolate, 2.2–5 by 0.8–2 mm, apex acuminate, pubescent outside; petals flabellate, 5–8 by 5–6 mm, base cuneately narrowed, somewhat claw-like, apex rounded; disc cupular, c. 0.3 mm wide, margin undulate, with deep notches; ovary c. 0.9 mm diam, glabrous, style c. 0.2 mm long, stigmas 0.8–1.2 mm long, apex slightly thickened and slightly bifid or not. Fruits c. 1.3 cm diam, green, glabrous; pedicel 1.7–2.65 cm long, 1–1.5 mm diam; sepals persistent but not accrescent; wall 0.6–0.8 mm thick, exocarp not detaching; columella 4.5–7 mm long. Seeds c. 7.5 by 6.5 mm diam; hilum rhombic, c. 1.5 by 1.5 mm.

Distribution — China (Mengla, Menglun, Yunnan), Laos (Luang Prabang).

Habitat & Ecology — Understorey in limestone mountains, often in humid habitats. Elevation: 600–850 m. Flowering: April to June, September; fruiting: May.

Note — The species can be distinguished from *T. eberhardtii* by the coriaceous, oblong leaves with very distinctive triplinerved venation and lacking oil dots.

17. *Trigonostemon longifolius* Baill. — sect. *Spinipollen* — Map 10

Trigonostemon longifolius Baill. (1858b) 23, pl. 11, f. 12 ('*longifolium*'); Müll. Arg. (1866) 1108; Kurz (1877b) 406 ('*longifolium*'); Hook.f. (1887) 396; Pax & K.Hoffm. (1911) 88, f. 28; Ridl. (1924) 264; Jabl. (1963) 162; Airy Shaw (1972) 347; Whitmore (1973) 136; Airy Shaw (1981) 355; Chantar. (2005) 26; (2007) 579, f. 94; R.Y.Yu & Welzen (2018) 197, f. 6. — [*Croton longifolius* Wall. (1847) nr. 7717, nom. nud., non Müll.Arg. (1873) 170.] — Lectotype (designated by Yu & Van Welzen 2018): *Wallich* 7717 (K, barcode K000959328; iso G, K, barcode K000959327), Malay Peninsula, Penang Island.

?*Athroisma dentatum* Griff. (1854a) 478 ('*dentatis*'); (1854b) pl. 585, f. 4. — Type: *Griffith s.n.?*, Nov. 1834 (K?), Myanmar, Mergui, Madamaca (see Hooker 1887: 396; Pax & Hoffmann 1911: 88).

?*Athroisma serratum* Griff. (1854a) 477 ('*serratis*'); (1854b) pl. 585, f. 9. — Type: *Griffith s.n.?* (K?), Myanmar, Mergui, Tenasserim [= Tanintharyi Region] (see Airy Shaw 1972: 347).

Prosartema gaudichaudii Gagnep. (1925a) 468, non *Trigonostemon gaudichaudii* (Baill.) Müll.Arg. (1865) 213. — *Trigonostemon gagnepainianus* Airy Shaw (1978) 415. — Syntypes: *Gaudichaud* 167 (P, barcodes P00717170, P00712171), Vietnam, Tourane; *Poilane* 8306 (P, barcode P00717169), Vietnam, km 26 from Nhatrang to Ninh Hoa; *Poilane* 10220 (NY*, barcode NY00273185, P, barcodes P00717158, P00717159), Vietnam, Quang Tri, Dent du Tigre; *Poilane* 10446 (K, P, barcodes P00717166, P00717167, P00717168), Vietnam, Quang Tri, Mai Lanh.

Trigonostemon howii Merr. & Chun (1935) 262; H.S.Kiu (1996) 163; P.T.Li et al. (2006) 118; P.T.Li & M.G.Gilbert (2008) 273. — Type: *How* 70940 (A, barcode A00048863, IBK, barcode IBK00169510, K, barcode K000959338, KUN, barcode KUN0403446, NY, barcode NY00273342, PE, barcode PE01110915, US, barcode US00096534), China, Hainan, Yaichow [= Yazhou], Licai [according to the duplicate in IBK] / Luopeng [according to the duplicates in KUN and PE].

Trigonostemon honbaensis Tagane & Yahara in Tagane et al. (2017) 39, syn. nov. — Type: *Toyama, Dang, Tagane, Fuse, Yahara, Nagamasu, Tran, Nguyen, Nguyen, Do, Ho* V1345 (holo KYO*; iso FU, not seen, VNM, not seen, the herbarium of Hon Ba Nature Reserve, not seen), Vietnam, Khanh Hoa Province, Mt Hon Ba.

Description — See Yu & Van Welzen 2018.

Distribution — China, Myanmar (Tenasserim), Thailand, Laos, Vietnam, Malay Peninsula, Sumatra, Borneo, Philippines.

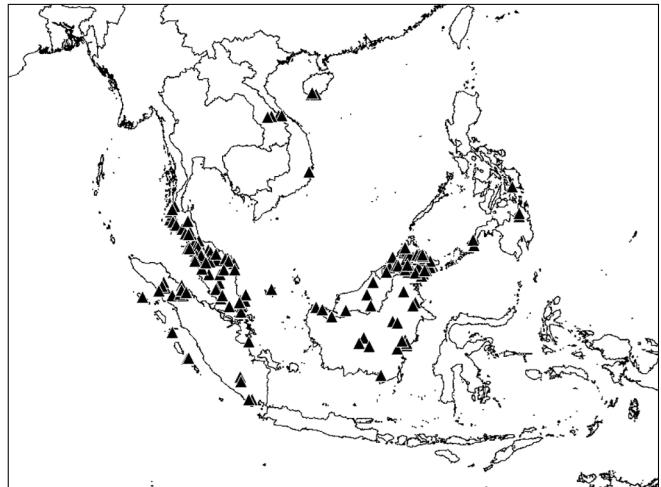
Note — The species was considered present in India because one of its syntypes, *Helper* KD 4798, was probably collected from Tenasserim (Myanmar) or the Andamans (India). We examined the duplicate in CAL, and confirmed that the specimen was collected from Tenasserim (not the Andamans), thus India is excluded from the distribution of the species. For more notes of the species, see Yu & Van Welzen 2018.

18. *Trigonostemon malaccanus* Müll.Arg. — sect. *Trigonostemon* — Map 11

Trigonostemon malaccanus Müll.Arg. (1864a) 482; (1866) 1110; Hook.f. (1887) 396; Pax & K.Hoffm. (1911) 90; Ridl. (1924) 265; Jabl. (1963) 154; Whitmore (1973) 136; Airy Shaw (1981) 355; R.Y.Yu & Welzen (2018) 201, f. 8. — Type: *Griffith* KD 4782 (K, barcode K000959325), Malay Peninsula, Malacca.

Trigonostemon laetus Baill. [(1858a) 341 ('*laetum*'), nom. nud.] ex Müll.Arg. (1866) 1109; Kurz (1877b) 407; Hook.f. (1887) 397; Pax & K.Hoffm. (1911) 90; N.P.Balakr. & Chakrab. (1991) 619, f. 6, syn. nov. — Syntypes: *Wallich* 7740B (G-DC*, barcodes G00319769, G00319757, on 3 sheets, P, barcodes P00717111, P00717112; isosyn CAL, barcode CAL0000023673), Myanmar, Amherst.

Description — See Yu & Van Welzen 2018.



Map 10 Distribution of *Trigonostemon longifolius* Baill.

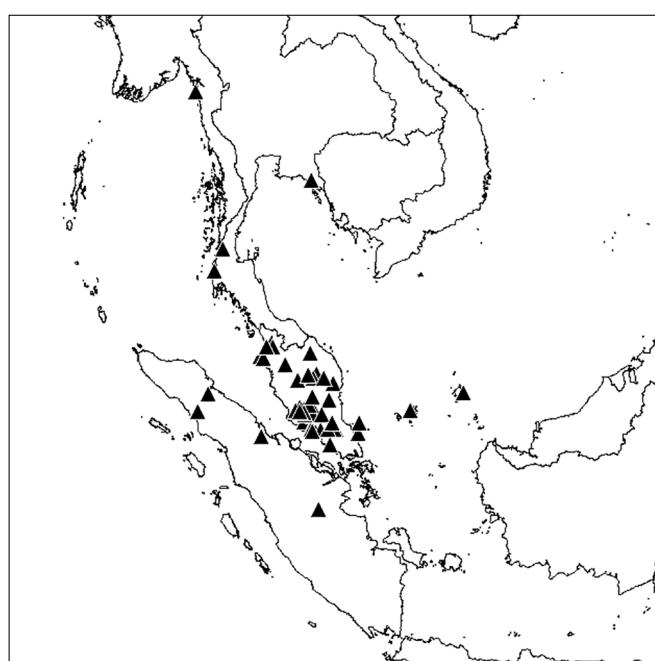
Distribution — Myanmar (Amherst), Thailand, Malay Peninsula, Sumatra.

Note — The name *Trigonostemon laetus* was referred to by Baillon (1858a) without any description. It was validated by Müller (1866), later than Müller's (1864a) description of *T. malaccanus*.

19. *Trigonostemon montanus* R.Y.Yu & Welzen, sp. nov. — sect. *Tylosepalum* — Fig. 3; Map 6

Trigonostemon montanus R.Y.Yu & Welzen resembles *T. lii* Y.T.Chang in the oblong leaves, which remain green when dry, but differs in having shorter and dichotomously branching inflorescences. — Type: *Koelz* 27903 (holo L, barcode L.2260526), India, Assam, Cachar, Laikul, 6000 ft, 6 May 1951. Paratypes: *Koelz* 27849 (L, barcode L.2260525), India, Assam, Cachar, Laikul, 4000 ft, 1 May 1951; *Bor* 2783 (K), India, Assam, Naga Hill, 5000 ft, 26 Apr. 1935.

Shrubs, 1.8–2.4 m tall; flowering branches 1–1.6 mm diam, pubescent when young, glabrous in old parts. Outer bark c. 0.1 mm thick, pale brown to grey; inner bark 0.1–0.2 mm thick, white or very light green when young, sap not seen; wood white. Stipules subulate, 0.2–0.4 mm long, caducous, often pubescent at base. Leaves: petiole terete but grooved above, 0.35–1 cm long, 0.7–1.5 mm diam, slightly pubescent when young, glabrescent; blade oblong, 6.2–11.8 by 1.4–2.7 cm, chartaceous, base acute, 2 adaxial glands present, margin entire or distantly serrate, teeth glandular, apex caudate, both surfaces glabrous but lower pubescent when young; venation triplinerved, slightly pubescent beneath, midrib slightly raised above and elevated beneath, secondary veins 5–7 pairs, bow-shaped and connected along margin, tertiary veins scalariform, veinlets reticulate, obscure. Inflorescences bisexual, terminal or subterminal thyrses; axis terete, dichotomously branching, 7.5–9 mm long, 0.5–1 mm diam, pubescent; bracts triangular, 0.2–1 by 0.2–0.45 mm, pubescent. Staminate flowers c. 3.2 mm diam; pedicel 4.5–5 mm long, 0.15–0.2 mm diam, glabrescent; sepals elliptic to lanceolate, 0.8–1.5 by 0.7–1.1 mm, base connate, margin entire, apex rounded to acute, pubescent outside; petals elliptic, 3.4–4.8 by 1.8–2.7 mm, contort, membranous, yellow to orange, glabrous; disc annular, c. 0.7–0.8 mm wide, with some irregular notches in margin, fleshy; stamens 3, androphore c. 1.5 mm long, c. 0.3 mm diam, anthers ellipsoid, 0.5–0.6 mm long. Pistillate flowers and fruits not seen.



Map 11 Distribution of *Trigonostemon malaccanus* Müll.Arg.

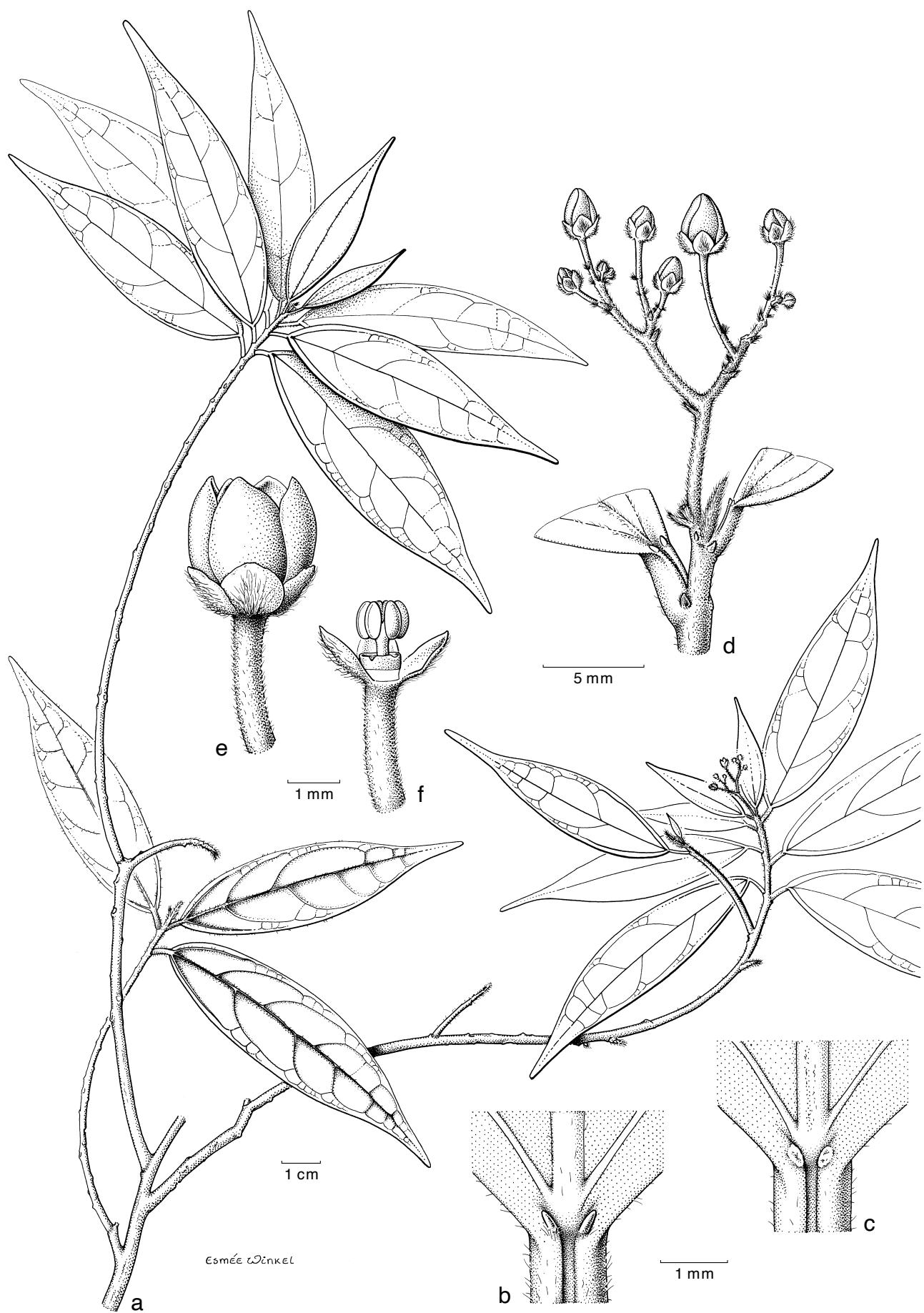


Fig. 3 *Trigonostemon montanus* R.Y.Yu & Welzen. a. Growing habit; b. leaf base, showing adaxial glands; c. leaf base, adaxial glands fallen; d. staminate inflorescence; e. staminate flower; f. staminate flower, petals and 2 sepals removed, showing the androphore and disc (all: Koelz 27903, barcode L.2260526). — Drawing by Esmée Winkel, 2019.

Distribution — India (Assam, endemic).

Habitat & Ecology — In forests. Elevation: 1200–1850 m. Flowering: April to May.

Notes — 1. Within the genus this species grows at perhaps the highest elevation.

2. The new species also resembles *T. inopinatus* from Australia in the short and dichotomously branching staminate inflorescences, but differs in having a distinctively triplinerved venation.

20. *Trigonostemon murtonii* Craib — sect. *Trigonostemon* — Map 8

Trigonostemon murtonii Craib (1911) 464 ('*murtonii*'); Pax & K.Hoffm. (1912) 128; Airy Shaw (1972) 347; Chantar. (2005) 26; (2007) 581. — Type: *Murton 18* (K, barcode K000959311), Thailand, west coast, Koh Klone.

Trigonostemon pierrei Gagnep. (1922) 752; (1925b) 321, syn. nov. — Type: *Pierre 1530* (A*, barcode A00048875, K, barcode K000959307, P, barcodes P00717121, P00717122, P00717123, US*, barcode US00096541), Vietnam, Phu Quoc, Mt Ong Chao.

Trigonostemon pinnatus Gagnep. (1922) 752; (1925b) 318. — Type: *Pierre s.n.* (K, barcodes K000959309, K000959310, P, barcodes P00717124, P00717125, P00717126, NY*, US*), Vietnam, Cochinchina, prov. de Bien Hoa, Mt Lap-vo

Shrubs, 1–5 m tall; flowering branches 1.1–3.5 mm diam, pubescent when young, glabrous in old parts. *Outer bark* c. 0.1 mm thick, dark brown to pale grey; inner bark c. 0.1 mm thick, reddish brown; wood pale yellowish. *Stipules* subulate, 0.3–0.7 mm long, caducous, often pubescent at base. *Leaves*: petiole terete but grooved above, 0.4–1.5 cm long, 0.8–2.2 mm diam, slightly pubescent; blade elliptic to oblanceolate, 6.5–19 by 1.9–5.2 cm, thick-chartaceous, base cuneately narrowed, 2 adaxial glands present, falcate, 0.7–1.2 mm long, margin distantly serrate, teeth falcate, apex acute to acuminate, glabrescent above and glabrous beneath; venation pinnate, midrib flat or slightly raised above, elevated beneath, secondary veins 8–13 pairs, bifurcate and connected along margin, tertiary veins and veinlets reticulate. *Inflorescences* seemingly unisexual, axillary or terminal; staminate ones racemose thyrses; axis 5.2–15 cm long, narrowing toward apex, basally 1.5–2 mm diam, pubescent; bracts lanceolate, 0.5–4 by 0.3–1 mm, pubescent; pistillate ones racemes, axis 3–9.5 cm long, 1.1–2.1 mm diam, pubescent, bracts triangular to lanceolate, 1.3–2.6 by 0.5–1 mm, pubescent. *Staminate flowers* 3.7–4.7 mm diam; pedicel 2.5–3.8 mm long, 0.15–0.2 mm diam, pubescent; sepals lanceolate, 1.2–1.5 by 0.7–0.8 mm, base connate, apex acute, sometimes with an indistinct apical appendage, pubescent outside; petals obovate, 1.2–2.1 by 1.1–1.4 mm; disc seemingly absent; stamens 3, sessile (filaments absent), anthers adhere to a conical mass formed by connectives, thecae ellipsoid, 0.4–0.5 mm long. *Pistillate flowers* (fruiting) 3.8–6.8 mm diam; pedicel 4.2–5.5 mm long, thickening toward apex, apically 0.8–1.8 mm diam; sepals lanceolate, 2–3.7 by 1–2.2 mm, pubescent, often with a protruding apical appendage outside; petals not seen, caducous; disc lobes semi-orbicular, c. 0.5 by 0.6–0.9 mm; ovary (fruiting) 3.2–4.5 mm diam, pubescent and warty, style absent, stigmas ligular, bifid, 0.8–0.9 mm long, flat at apex, 0.8–0.95 mm wide. *Fruits* (young) 5.4–6 mm diam, pubescent and significantly warty; sepals persistent but not accrescent; wall 5–7 mm thick, exocarp not detaching; columella 4.2–6.3 mm long. *Seeds* globose, 5.6–6.2 by 5.1–6 mm, marbled; hilum elliptic to heart-shaped, 1.2–1.5 by 1–1.5 mm.

21. *Trigonostemon nemoralis* Thwaites — sect. *Pycnanthera* — Map 5

Trigonostemon nemoralis Thwaites (1861) 277; Müll.Arg. (1866) 1108; Hook.f. (1887) 398; Trimen (1898) 51; Bourd. (1908) 504; Pax & K.Hoffm. (1911) 93; Gamble (1925) 1341; N.P.Balakr. & Chakrab. (1991) 623, f. 8; Philcox (1997) 111. — Lectotype (designated here): *Thwaites CP 3570* (K, barcode K000246867; iso A*, barcode A00048874, CAL, barcodes CAL0000023670, CAL0000023671, FR*, barcode FR0036074, G-DC*, barcodes G00319812, G00319788, GH*, barcode GH00048873, K, barcodes K000246866, K000246868, K000246869, NY*, barcode NY00273343, P, barcodes P00717116, P00717117, P00717118), Sri Lanka, Central Province, Madamahanewera.

Shrubs or small trees; flowering branches 1.5–2.6 mm diam, pubescent when young, glabrous in older parts. *Outer bark* c. 0.1 mm diam, pale brown; inner bark 0.1–0.2 mm thick, dark red to reddish brown; wood brown. *Stipules* lanceolate to linear to subulate, 1.5–4.2 by 0.2–0.8 mm, pubescent. *Leaves*: petiole terete but grooved above, 0.4–1.5 cm long, 0.8–2.2 mm diam, slightly pubescent; blade elliptic to oblanceolate, 6.5–19 by 1.9–5.2 cm, thick-chartaceous, base cuneately narrowed, 2 adaxial glands present, falcate, 0.7–1.2 mm long, margin distantly serrate, teeth falcate, apex acute to acuminate, glabrescent above and glabrous beneath; venation pinnate, midrib flat or slightly raised above, elevated beneath, secondary veins 8–13 pairs, bifurcate and connected along margin, tertiary veins and veinlets reticulate. *Inflorescences* seemingly unisexual, axillary or terminal; staminate ones racemose thyrses; axis 5.2–15 cm long, narrowing toward apex, basally 1.5–2 mm diam, pubescent; bracts lanceolate, 0.5–4 by 0.3–1 mm, pubescent; pistillate ones racemes, axis 3–9.5 cm long, 1.1–2.1 mm diam, pubescent, bracts triangular to lanceolate, 1.3–2.6 by 0.5–1 mm, pubescent. *Staminate flowers* 3.7–4.7 mm diam; pedicel 2.5–3.8 mm long, 0.15–0.2 mm diam, pubescent; sepals lanceolate, 1.2–1.5 by 0.7–0.8 mm, base connate, apex acute, sometimes with an indistinct apical appendage, pubescent outside; petals obovate, 1.2–2.1 by 1.1–1.4 mm; disc seemingly absent; stamens 3, sessile (filaments absent), anthers adhere to a conical mass formed by connectives, thecae ellipsoid, 0.4–0.5 mm long. *Pistillate flowers* (fruiting) 3.8–6.8 mm diam; pedicel 4.2–5.5 mm long, thickening toward apex, apically 0.8–1.8 mm diam; sepals lanceolate, 2–3.7 by 1–2.2 mm, pubescent, often with a protruding apical appendage outside; petals not seen, caducous; disc lobes semi-orbicular, c. 0.5 by 0.6–0.9 mm; ovary (fruiting) 3.2–4.5 mm diam, pubescent and warty, style absent, stigmas ligular, bifid, 0.8–0.9 mm long, flat at apex, 0.8–0.95 mm wide. *Fruits* (young) 5.4–6 mm diam, pubescent and significantly warty; sepals persistent but not accrescent; wall 5–7 mm thick, exocarp not detaching; columella 4.2–6.3 mm long. *Seeds* globose, 5.6–6.2 by 5.1–6 mm, marbled; hilum elliptic to heart-shaped, 1.2–1.5 by 1–1.5 mm.

Distribution — India (Travancore), Sri Lanka.

Habitat & Ecology — Flowering: February to June.

Note — The species resembles *T. diplopetalus* and *T. longifolius*, but can be distinguished from the former by the apical gland on the sepals (vs without the apical gland; but check multiple sepals) and from the latter by the sessile stamens (vs androphore c. 0.4 mm long).

22. *Trigonostemon pachyphyllus* Airy Shaw — sect. *Trigonostemon* — Map 3

Trigonostemon pachyphyllus Airy Shaw (1971) 546; (1972) 347; Chantar. (2005) 27; (2007) 581. — Type: *Kerr 19429* (holo K, barcode K000959302), Thailand, Trang, Khao Soi Dao.

Shrubs, c. 1.5 m tall; flowering branches 3.2–4 mm diam, glabrescent. *Outer bark* c. 0.1 mm thick, brown; inner bark 0.1–0.2 mm thick, reddish brown; wood yellow. *Stipules* subulate, 0.6–0.8 mm long, caducous, pubescent. *Leaves*: petiole wrinkled,

Distribution — Thailand, Cambodia, Vietnam.

Habitat & Ecology — Evergreen forests, on sandy clay. Elevation: c. 250 m. Flowering: February, April, June, November; fruiting: April.

Note — The inflorescences are often racemose when young and start branching and become apically broom-like when older. In this character it resembles *T. scopulatus* R.Y.Yu & Welzen, but that species has a much longer petiole.

flat or slightly grooved above, 0.3–1 cm long, 2–2.2 mm diam, pubescent to glabrous; blade oblong, 12–19 by 2.1–3.9 cm, coriaceous, base acute, adaxial glands not seen, margin entire, occasionally with very sparse glandular teeth, apex acuminate, upper surface glabrous, dull green or pupilish brown when dry, lower surface sparsely pubescent, yellow when dry; venation pinnate, midrib flat above and elevated beneath, often pubescent beneath, secondary veins 12–15 pairs, curved, bifurcate and connected along margin, tertiary veins reticulate. Inflorescences seemingly unisexual; staminate ones axillary, thyrses, axis 1–1.4 cm long, 0.8–1.1 mm diam, pubescent, bracts triangular, 0.15–1.3 by 0.2–0.6 mm, pubescent; pistillate ones terminal or axillary, racemes, axis up to 1.5 cm long, 0.6–1.1 mm diam, pubescent, bracts lanceolate, 0.6–2.5 by 0.3–0.8 mm, pubescent outside. Staminate flowers at least 3.5 mm diam; pedicel c. 1.2 mm long, c. 0.35 mm diam, pubescent; sepals elliptic, 1–1.7 by 0.3–0.8 mm, base connate, margin entire, apex acute, pubescent or hirsute outside; petals obovate, 3.4–4.5 by 1.4–2.5 mm, dark red-purple, glabrous; disc lobes rectangular, 0.35–0.5 by 0.35–0.45 mm, apex truncate to slightly rounded; stamens 5, anthers ellipsoid, 0.8–1 mm long, apically divaricate. Pistillate flowers (fruiting) 6–10.5 mm diam; pedicel thickening toward apex, 3.6–4.5 mm long, apically 1.5–2 mm diam, pubescent; sepals triangular to lanceolate, 8.5–10 by 3.5–4.6 mm, outer surface pubescent, sometimes marbled, mixed patches in dark red and yellow, inner surface glabrous, dark purplish red when dry, base connate, margin distantly serrate, teeth glandular, apex acuminate, ending in a gland; petals fallen, not seen; disc lobes semi-orbicular, 0.7–0.9 by 0.45–0.6 mm, apex rounded; ovary c. 1.5 mm diam, densely pubescent; style c. 0.2 mm long; stigmas apically deeply bifid, free arms 0.5–0.6 mm long. Fruits c. 1 cm diam, green; sepals persistent, green. Seeds not seen.

Distribution — Thailand (Trang and Phatthalung, endemic).

Habitat & Ecology — Evergreen forests, understorey, near streams. Flowering: March to April; fruiting: April.

Note — A rare species endemic to Thailand. It resembles *T. capillipes* (Milne 1995) in the 5 stamens and relatively large pistillate sepals, and was treated as a synonym in our previous revision (Yu & Van Welzen 2018). However, after examining more collections, we reinstate the species here. The main spotting characters of *T. pachyphyllus* includes the coriaceous leaves (thick leaves as indicated by the specific epithet) and the discolored surfaces when dry. In addition, the pistillate sepals sometimes display a marbled pattern on the outer surface and the inflorescences are considerably smaller.

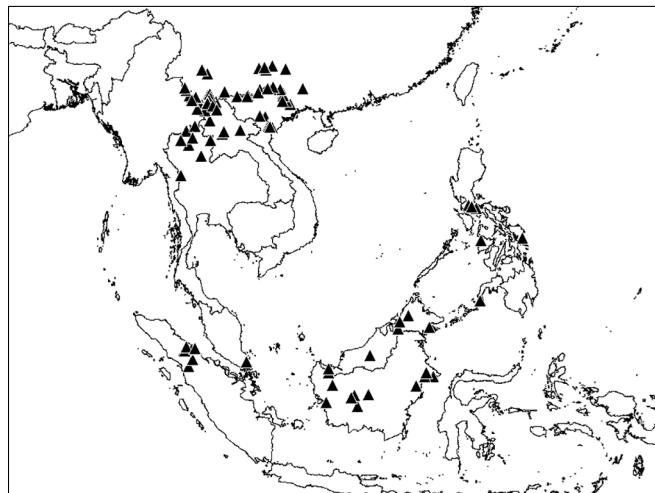
23. *Trigonostemon philippinensis* Stapf — sect. *Tylosepalum* — Map 12

Trigonostemon philippinensis Stapf (1907) 206 ('*philippinense*'); Pax & K.Hoffm. (1911) 91; Merr. (1923) 452; Airy Shaw (1981) 355; (1983) 47; R.I.Milne (1995) 27, in key, 29, in key. — Lectotype (designated here): Elmer 8326 (K, barcode K000959370; iso BO, sheet no. BO1298668, G, barcode G00435099, L, barcode L.2260355), Philippines, Luzon, Laguna prov., Los Baños, Mt Maquiling [= Mt Makiling].

Trigonostemon thyrsoides Stapf (1909) 264 ('*thyrsoides*'); Airy Shaw (1972) 348; H.S.Kiu (1996) 166; Chantar. (2005) 29; (2007) 584, pl. 32, 1; P.T.Li & M.G.Gilbert (2008) 274. — Type: Henry 11947 (A*, barcodes A00048871, A00048872, K, barcode K000959335, NY, barcode NY00273339), China, Yunnan, Simao (Szemao).

Trigonostemon laoticus Gagnep. (1922) 751. — *Prosartema laotica* Gagnep. (1925b) 306, syn. nov. — Type: *Thore* s.n. (P, barcodes P00717113, P00717114, P00717115), Laos, Luang-prabang.

Prosartema stellaris Gagnep. (1924) 875; (1925b) 304. — *Trigonostemon stellaris* (Gagnep.) Airy Shaw (1978) 415, syn. nov. — Syntypes: *Balansa* 3322 (P, barcodes P00717163, P00717164, P00717165); *Balansa* 3323 (P, barcode P00717162); *Balansa* 3324 (P, barcodes P00717160, P00717161), Vietnam, Tokin, Langkok (Mt Bavi) valley.



Map 12 Distribution of *Trigonostemon philippinensis* Stapf.

Trigonostemon nigrifolius N.P.Balakr. & Chakrab. (1984b) 173; (1991) 625, f. 9, syn. nov. — Type: Po Khaut 12434 (holo DD*), Myanmar, Maymyo Dist., Gokteik viaduct.

Description — See Yu & Van Welzen 2018.

Distribution — Myanmar (Maymyo), China, Thailand, Laos, Vietnam, Malay Peninsula, Sumatra, Borneo, Philippines.

Note — *Trigonostemon nigrifolius* is only known from the type collection and is considered conspecific with *T. philippinensis* here. The black leaves and blackish crimson petals appear to be a drying artefact.

24. *Trigonostemon quocensis* Gagnep. — sect. *Tylosepalum* — Map 6

Trigonostemon quocensis Gagnep. (1922) 753; (1925b) 316; Airy Shaw (1972) 348; Chantar. (2005) 27; (2007) 582. — Lectotype (designated here): Pierre s.n. (P, barcode P00717135; iso K, barcode K000959314, P, barcodes P00717136, P00717138), Vietnam, Phu Quoc. — Other syntypes: Godefroy 739 (P, barcodes P00717131, P00717132), Vietnam, Ha-tien; Godefroy 740 (P, barcode P00717130), Vietnam, Ha-tien; Harmand 632 (P, barcodes P00717128, P00717129), Vietnam, Nui Cam; Pierre 6232 (G, barcode G00435097, MPU, barcodes MPU015001, MPU015002, NY, barcode NY00273345, P, barcodes P00717133, P00717134, P00717137), Vietnam, Chaudoc, Mount Pell.

Trigonostemon birmanicus Chakrab. & N.P.Balakr. (1984a) 175; N.P.Balakr. & Chakrab. (1991) 613, f. 2, syn. nov. — Type: Chin [collector's name uncertain] 5849 (holo CAL, barcode CAL0000023654), Myanmar, Upper Chindwin, Numpakom drainage.

Shrubs or small trees, 0.5–5 m tall, dhh 6–8 cm; flowering branches 1–3.8 mm diam, pubescent when young, glabrous in old parts. Indumentum of simple hairs; translucent (oil?) dots sometimes present in green parts. Outer bark 0.1–0.2 mm thick, dark brown; inner bark 0.1–0.2 mm thick, reddish brown, solidified sap reddish black; wood yellow. Stipules subulate, 0.2–0.7 mm long, caducous, sometimes pubescent at base. Leaves: petiole terete, (0.6–)1–6.1 cm long, 0.8–2 mm diam, glabrous or pubescent, sometimes thickened at apex and base; blade ovate to elliptic, 8–24 by 3.6–10 cm, chartaceous, base truncate, rounded, acute or sometimes cordate, 2 adaxial glands present, sometimes pubescent, margin distantly serrate, apex acuminate to caudate, both surfaces pubescent when young, glabrous when mature; venation triplinerved (basal secondary veins often as thick as other secondary veins), midrib and sometimes secondary veins flat or slightly raised above and distinctively elevated and pubescent beneath, other secondary veins 6–9 pairs, bow-shaped and connected along margin, tertiary veins scalariform, veinlets reticulate. Inflorescences bisexual, terminal or axillary, large panicles, pistillate flowers

open before staminate ones; main axis terete, up to 44 cm long, 0.6–1.5 mm diam, pubescent; bracts linear to lanceolate, 1–12 by 0.15–1(–2.1) mm, often pubescent. **Staminate flowers** 4.4–5.5 mm diam, buds usually globose; pedicel 3.5–7.5 mm long, 0.15–0.3 mm diam, glabrous; sepals ovate to elliptic, 1.4–2.5 by 0.8–2.2 mm, base connate, margin entire, apex acute to rounded, pubescent outside; petals obovate to flabellate, 2.1–3.9 by 1.7–2.5 mm, contort, yellow, lower part sometimes claw-like, apex rounded, glabrous; disc annular, fleshy, margin entire, 0.4 (inner margin)–0.8 mm (outer margin) diam; stamens 3, androphore 0.3–0.6 mm long, 0.2–0.3 mm diam, free part of filaments 0.4–0.5 mm long, anthers free, globose to ellipsoid, 0.4–0.5 mm long. **Pistillate flowers** 6–7 mm diam, buds somewhat conical; pedicel thickening toward apex, 2–5.5 mm long, apically 0.5–0.9 mm diam when flowering, elongating to 4–9 mm long, apically 0.6–1 mm diam when fruiting, pubescent; sepals lanceolate to elliptic, 1.5–4.5 by 0.7–1.6 mm, base connate, margin entire, apex acute to acuminate; petals and disc as staminate flowers; ovary 1–1.2 mm diam, densely pubescent, style indistinct, stigmas 0.4–1 mm long, slightly thickened and sometimes slightly bifid at apex. **Fruits** 1–1.1 cm diam, hirsute; sepals persistent, but not accrescent; wall 0.3–0.4(–0.5) mm thick, exocarp not detaching; columella 4.5–6.5 mm long. **Seeds** 6–7 mm diam, marbled; hilum orbicular or rhombic, 1.2–1.7 by 1.1–1.5 mm.

Distribution — Myanmar (Upper Chindwin, in Sagaing or Kachin region), Thailand, Vietnam.

Habitat & Ecology — Understorey in dry evergreen forests, on limestone. Elevation: 140–820 m. Flowering: all year round; fruiting: March, September.

Note — The species is relatively common in Thailand and Vietnam. Only two collections are known from Myanmar (*Chin?* 5849 and *Griffith KD 4741*). The plant sometimes has the similar translucent (oil?) dots in the green parts as *T. eberhardtii*. The staminate buds are usually globose (petals still contort), but in most other species they are often conical.

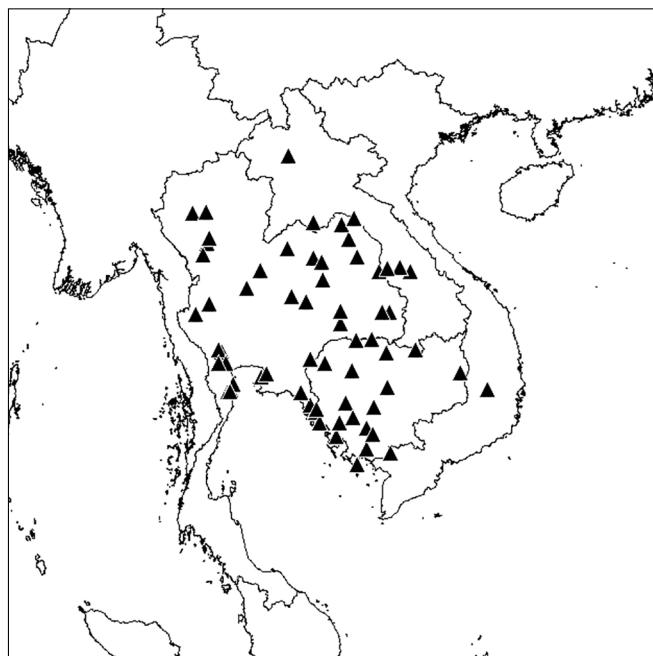
25. *Trigonostemon reidioides* (Kurz) Craib — sect. *Spinipollen* — Map 13

Trigonostemon reidioides (Kurz) Craib (1911) 464; Pax & K.Hoffm. (1912) 128; Gagnep. (1925b) 316; Airy Shaw (1972) 348; Chantar. (2005) 28; (2007) 582. — *Baliospermum reidioides* Kurz (1875) 32; (1877b) 411; Hook.f. (1887) 461; F.N.Williams (1905) 32; Pax & K.Hoffm. (1912) 29. — Lectotype (designated here): Teijsmann HB 5981 (K, barcode K000959313), Thailand, Kanburi [= Kanchanaburi]. — Other syntype: Teijsmann s.n. (CAL, barcode CAL0000023659), Thailand.

Trigonostemon hybridus Gagnep. (1922) 750, syn. nov.; (1925b) 318. — Lectotype (designated here): Pierre 6282 (P, barcode P00717109), Vietnam, Phu Quoc (other duplicates are syntypes cited under the next name).

Trigonostemon rubescens Gagnep. (1922) 754; (1925b) 317, syn. nov. — Lectotype (designated here): Thorel 2290 (P, barcode P00717140; iso NY*, barcode NY00273346, P, barcodes P00717141, P00717142, US*, barcode US00096544), Laos, Kong et île de Khon. — Other syntypes: Pierre 6281 (P, barcodes P00717139, P00648668, P00648669, P00648670), Cambodia, Kompong Spen, Mont Ramcon; Pierre 6282 (K, barcode K000959312, P, barcodes P00717143, P00717144, P00717145), Vietnam, Phu-Quoc.

Shrubs, 0.5–1.5 m tall; flowering branches 1.2–3.2 mm diam, slightly to densely pubescent. **Indumentum** of simple and stellately bundled hairs. **Outer bark** c. 0.1 mm thick, greyish to dark brown; inner bark 0.1–0.2 mm thick, dark reddish, sap clear, watery, black or dark red in dry material; wood yellow or brown. **Stipules** acicular to subulate, 0.6–2.3 mm long, caducous, pubescent at base. **Leaves**: petiole terete, slightly grooved above, 0.5–2.5 cm long, 0.6–1.9 mm diam, densely pubescent to glabrescent; blade oblong to elliptic, rarely obovate or (ob)lanceolate, 3.5–15 by 0.5–6.3 cm, chartaceous to coriaceous, base acute to rounded, adaxial glands 2, falcate, blackish, margin entire, apex acute to acuminate, upper surface



Map 13 Distribution of *Trigonostemon reidioides* (Kurz) Craib.

dull dark green, lower surface dull light green, both surfaces densely to slightly pubescent, when slightly pubescent then often only simple hairs present; venation triplinerved, pubescent on both sides, midrib and basal secondary veins flat above and elevated below, other secondary veins 2–8 pairs, bow-shaped and connected along margin, tertiary veins and veinlets reticulate. **Inflorescences** bisexual, axillary or terminal large panicles; main axis terete, 3–29 cm long, 0.4–1.2 mm diam, dull red, often pubescent, rarely glabrescent; bracts lanceolate to linear, 0.5–17 by 0.1–1.9 mm, pubescent. **Staminate flowers** 4.1–6.6 mm diam; pedicel 2.5–7 mm long, 0.15–0.5 mm diam, pale light green to dull reddish, pubescent to glabrescent; sepals elliptic, 1–2.6 by 0.5–1.6 mm, pale light green to dull light yellow or reddish, base connate, margin entire, sometimes ciliate, apex acute to rounded, pubescent to glabrescent outside; petals obovate to spatulate, 3.3–6.4 by 1.6–4.2 mm, white, dark red, deep maroon or dark purple, lower part sometimes claw-like, apex rounded, glabrous; disc annular, somewhat plicate, light orange, glabrous, margin undulate, 0.3–0.45 mm wide; stamens 3, androphore 0.35–0.7 mm long, 0.2–0.5 mm diam, cream, anthers ellipsoid, 0.5–0.8 mm long, cream. **Pistillate flowers** 5.3–8.9(–13) mm diam; pedicel slightly thickening toward apex, 8–20 mm long, apically 0.4–1 mm diam when flowering, elongating in fruit to (0.8–)1.6–3.4 cm long, apically 0.7–1.5 mm diam, pubescent, glabrescent; sepals elliptic to oblong, 3–6 by 1.1–2.2 mm, base connate, margin entire, sometimes ciliate, apex acute to acuminate, pubescent outside; petals as staminate flowers but larger, 5.9–9 by 2.6–6 mm; disc as staminate flowers; ovary 1.3–1.6 mm diam, pubescent, light yellow or green, style absent, stigmas thickening toward apex, 0.7–0.8 mm long, apically 0.5–0.6 mm wide, white, pale light yellow or cream, furrowed above, apically not bifid. **Fruits** 1–1.3 cm diam, green, pubescent; sepals persistent but not accrescent; wall 0.4–0.6 mm thick, exocarp partly detaching; columella 4.2–5.8 mm long. **Seeds** 4.6–6.3 mm diam, often marbled; hilum oblong to elliptic to triangular, 0.7–1.8 by 0.5–1 mm.

Distribution — Thailand, Laos, Cambodia, Vietnam.

Habitat & Ecology — Often in open areas in dry dipterocarp forests, or in seasonal deciduous pine or *Melaleuca* forests, occasionally in waste lands or swampy forests. Often growing in sandy or rocky soil, sometimes along roads or rivers. Eleva-

tion: 20–300 m. Flowering: all year round; fruiting: January to June, August, October.

Notes — 1. This is a common species in Thailand and Indochina. The species displays a continuous variation in the indumentum: from very dense stellately bundled hairs (as represented by the type collection of *T. reidiooides*) to relatively sparse and mostly simple hairs (but stellately bundled hairs are still present; as in the type collections of *T. rubescens*). *Trigonostemon hybridus* represents an intermediate form between the above mentioned two, and Gagnepain (1922) even considered it as a hybrid form. As morphological discontinuities are lacking, *T. hybridus* and *T. rubescens* are placed in synonymy. Only two species of *Trigonostemon* (the other species is *T. balgooyi* R.Y.Yu & Welzen from Johor, Malaysia) have an indumentum of both simple and stellately bundled hairs, making it a useful character in identification.

2. Several specimens (probably ‘duplicates’) are present under the collection number *Pierre* 6282. Of these specimens, one was identified as *T. hybridus* and the others as *T. rubescens*. In order to avoid confusion, we select *Pierre* 6282 (P, barcode P00717109) as the lectotype of *T. hybridus* (based on the specimen label) and the other specimens under this number are cited as syntypes of *T. rubescens*. *Thorel* 2290 (P, barcode P00717140) is selected as the lectotype of *T. rubescens*.

26. *Trigonostemon semperflorens* (Roxb.) Müll.Arg. — sect. *Trigonostemon* — Map 7

Trigonostemon semperflorens (Roxb.) Müll.Arg. (1866) 1110; Hook.f. (1887) 397; Brandis (1906) 580; Pax & K.Hoffm. (1911) 90; Kanjilal et al. (1940) 196; N.P.Balakr. (1983) 427. — *Clutia semperflorens* Roxb. (1832) 730; Voigt (1845) 155. — *Silvea hookeriana* Baill. (1858a) 342, nom. superfl. — *Trigonostemon hookerianus* (Baill.) Müll.Arg. (1866) 1109, nom. superfl. — Lectotype (designated by Yu et al. 2019): Roxburgh’s Flora Indica drawing, no. 2401 (CAL).

Small trees, 1–2.5 m tall; flowering branches 2.2–4.4 mm diam, pubescent when young, glabrous in older parts. Outer bark 0.1–0.2 mm thick, pale brown; inner bark 0.1–0.2 mm thick, dark red; wood pale yellow, pith hollow. *Stipules* subulate, 0.7–2.5 mm long, caducous. *Leaves*: petiole terete but often furrowed above, 2.5–9 mm long, 1.5–2.7 mm diam, pubescent; blade oblanceolate, cuneately narrowed in lower part, 8–32 by 2.8–5.9 cm, chartaceous, base abruptly rounded to truncate, adaxial glands not seen, margin distantly serrate, teeth falcate when young, glandular or nipple-like when mature, apex acuminate to caudate, both surfaces glabrous; venation pinnate, midrib elevated and slightly pubescent on both sides, secondary veins 12–18 pairs, tertiary veins reticulate. *Inflorescences* unisexual or bisexual, rami- and cauliflorous, in short cymes or thyrses, or a single to a few flowers on short brachylasts; peduncle 1.5–11 mm long, 0.5–0.9 mm diam, pubescent; bracts oblong to lanceolate, 0.3–5.6 by 0.2–1 mm, pubescent. *Staminate flowers* 3.8–4.9 mm diam; pedicel 2.2–2.5 mm long, 0.2–0.3 mm thick, glabrous; sepals elliptic, often unequal, 1–1.8 by 0.8–1.3 mm, base connate, margin entire, sometimes slightly ciliate, apex acute to rounded, pubescent outside; petals obovate to elliptic, 1.8–2.8 by 1.1–1.8 mm, base claw-like, apex rounded, glabrous, purple; disc lobes trapezoid, 0.2–0.3 by 0.2–0.25 mm, recurved at apex, glabrous; stamens 3, androphore 0.5–0.6 mm long, c. 0.1 mm diam; anthers free, divaricate at apex, thecae 0.4–0.5 mm long, connective with numerous droplets with secretion. *Pistillate flowers* (fruiting) 4.2–5.3 mm diam; pedicel c. 1 mm long, c. 0.5 mm diam when flowering, elongating in fruit to 2.5–4 mm long, 1.2–1.4 mm diam, glabrous to slightly pubescent; sepals elliptic to lanceolate, 1.1–2.5 by 0.65–1.2 mm when flowering, slightly accrescent to c. 5 by 2.1 mm when fruiting, base connate, margin entire or with 2 apical teeth, apex acute, pubescent outside; petals elliptic, c. 3.2 by

1.7 mm, base claw-like, apex rounded; disc not seen; ovary 1.5–1.8 mm diam, densely pubescent, stigmas 0.4–0.5 mm long, apically deeply bifid. *Fruits*: sepals persistent; columella 4–6 mm long. Seeds not seen.

Distribution — NE India, Bangladesh.

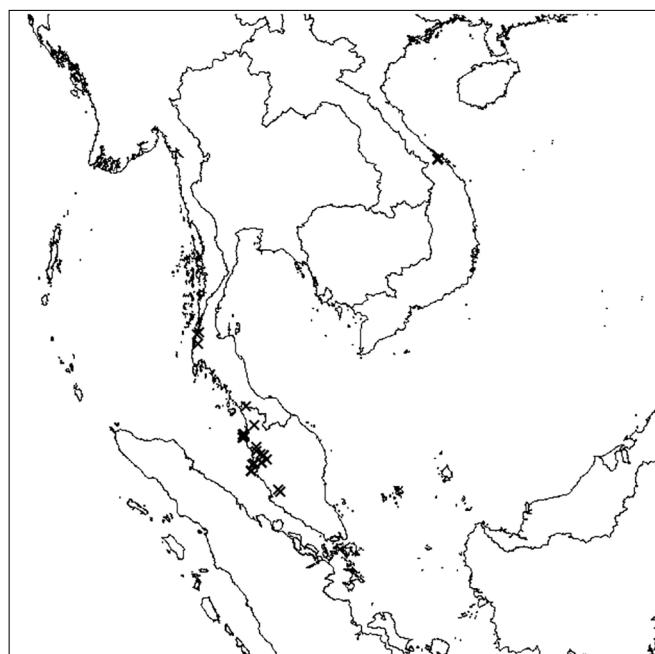
Habitat & Ecology — In forests. Elevation: 670–1000 m. Flowering: May.

Note — See note under *T. flavidus*.

27. *Trigonostemon tuberculatus* F.Du & Ju He — sect. *Tylosepulum* — Map 3

Trigonostemon tuberculatus F.Du & Ju He in Du et al. (2010) 111, f. 1, 2. — Type: Du, He & Zhang 200401 (holo SWFC, not seen), China, Yunnan, Yuanjiang.

Shrubs, up to 2 m tall; flowering branches 2.3–2.5 mm diam, densely pubescent. *Bark* 0.1–0.2 mm thick, pale brown; wood yellow to brown. *Stipules* subulate, 0.5–0.7 mm long, caducous, densely pubescent at base, often buried in hairs. *Leaves*: petiole terete, 1.4–3.3 cm long, 0.8–1 mm diam, densely pubescent; blade ovate, 4.4–6.9 by 1.6–4.7 cm, coriaceous, base acute to truncate, 2 adaxial glands present, margin distantly serrate, teeth glandular, apex acute, both surfaces densely pubescent; venation often palmate, densely pubescent on both sides; midrib and basal secondary veins slightly elevated on both surfaces, other secondary veins 5–7 pairs, bifurcate and connected along margin, tertiary veins scalariform, obscure, veinlets reticulate, obscure. *Inflorescences* seemingly unisexual, axillary or terminal panicles; main axis terete, 2.7–5 cm long, 0.5–1 mm diam, densely pubescent; bracts lanceolate, 0.8–1.8 by 0.5–0.8 mm, densely pubescent. *Staminate flowers* 4.1–6.1 mm diam; pedicel 1.6–2.7 mm long, 0.3–0.5 mm diam, densely pubescent; sepals elliptic, 1.5–3 by 0.9–1.5 mm, base connate, margin entire, apex acute, pubescent outside; petals spathulate, 3–3.8 by 1.4–2 mm, apex rounded, yellow, glabrous; disc annular, c. 0.4 mm wide, pubescent; stamens 3, androphore 0.9–1 mm long, 0.15–0.2 mm diam, anthers ellipsoid, 0.6–0.7 mm long. *Pistillate flowers* (Du et al. 2010): sepals elliptic, c. 3 mm long, with buff vesicles, densely tomentose outside; petals narrowly elliptic, c. 4 mm long, glabrous, with or without 1–2 dichotomous glands; disc unknown; ovary tuberculate, densely



Map 14 Distribution of *Trigonostemon verticillatus* (Jack) Pax. var. *verticillatus*.

long tomentose, stigmas bifid at apex. *Fruits* (Du et al. 2010) oblate, c. 3 cm diam, green when young, warts 1–2 mm diam. *Seeds* (Du et al. 2010) flat, elliptic, 0.9–1 cm long, c. 0.6 mm diam; aril c. 1 mm thick, spongy, green.

Distribution — China (Yuanjiang, Yunnan; endemic).

Habitat & Ecology — On hill slopes, on the banks of the Yuanjiang river, in arid areas. Elevation: c. 300 m. Flowering: March.

Notes — 1. The species has a few very unusual characters: it is the only species known to have a pubescent disc; the fruits are very warty and exceptionally large; the seeds have a green aril (Du et al. 2010).

2. We have only seen one collection of the species; the description of pistillate flowers, fruits and seeds is based on Du et al. 2010. The colour of the staminate petals (yellow) was known from photos by Si-Yu Zhang posted on Plant Photo Bank of China (<http://ppbc.ipplant.cn/>).

28. *Trigonostemon verticillatus* (Jack) Pax var. *verticillatus*

— sect. *Trigonostemon* — Map 14

Trigonostemon verticillatus (Jack) Pax in Pax & Hoffmann (1911) 87; Jabl. (1963) 164; Airy Shaw (1972) 349; Whitmore (1973) 136; Chantar. (2005) 30; (2007) 585, pl. 31, 2; R.Y.Yu & Welzen (2018) 213. — *Enchidium verticillatum* Jack (1822) 90; (1835) 257, excl. synon. Rumphius; Müll. Arg. (1866) 1256; Merr. (1952) 224. — Neotype (designated by Yu & Van Welzen 2018): *Maingay* 1403 (L, barcode L.2258683; isoneo: BM, CAL, barcode CAL0000031928, K), Malay Peninsula, Malacca.

Telogyne indica Baill. (1858a) 328; (1858b) pl. 11, f. 13. — *Trigonostemon indicus* (Baill.) Müll.Arg. (1865) 214; (1866) 1107; Hook.f. (1887) 398; Ridl. (1924) 264; Jabl. (1963) 152. — Lectotype (designated by Yu & Van Welzen 2018): *Wallich* 7997 (G*, barcode G00435096; iso G*, no barcode; G-DC*, barcode G00319770, on 2 sheets, K, barcodes K000959330, K000959331, K000959332, K000959333, P, barcode P00717110), Malaysia, Penang.

Description & Taxonomic notes — See Yu & Van Welzen 2018.

Distribution — Thailand, Malay Peninsula.

29. *Trigonostemon villosus* Hook.f. var. *nicobaricus* (Chakrab.) N.P.Balakr. & Chakrab. — sect. *Trigonostemon* — Map 8

Trigonostemon villosus Hook.f. var. *nicobaricus* (Chakrab.) N.P.Balakr. & Chakrab. (1991) 629. — *Trigonostemon nicobaricus* Chakrab. (1984) 203. — Type: *Dwivedi* 8521 (holo 8521A CAL, barcode CAL0000023667, iso 8521B, 8521C, 8521D, 8521E, PBL, not seen), India, Great Nicobar Island, 9 km on East-West road.

Small trees, 5–7 m tall; flowering branches 2.8–3.8 mm diam, pubescent when young. Outer bark c. 0.1 mm thick, flaky, pale brownish; inner bark c. 0.1 mm thick, dark reddish; wood pale yellow. *Stipules* subulate, 0.8–1 mm long, caducous. *Leaves*: petiole terete but grooved above, 0.3–1 cm long, c. 2.3 mm diam, pubescent; blade oblanceolate, 6.5–23.8 by 2.1–5.6 cm, chartaceous, base abruptly narrowed, rounded to obtuse, 2 adaxial glands present, margin distantly serrate, apex acuminate to caudate, upper surface glabrescent, slightly pubescent beneath; venation pinnate; midrib slightly raised above and elevated beneath, secondary veins 13–18 pairs, slightly curved and connected along margin, tertiary veins reticulate. *Inflorescences* unisexual, terminal or axillary, staminate ones racemose thyrses, pistillate ones racemes; axis up to 4.8–11.7 cm long, 0.4–0.6 mm diam, slightly pubescent; bracts lanceolate to elliptic, 1.5–7 by 0.4–0.7 mm, pubescent outside. *Staminate flowers* (Chakrabarty 1984): pedicel 2–5 mm long, apically 0.4–0.7 mm diam, basally 0.1–0.3 mm diam, puberulous; sepals oblong to triangular, 1–1.5 by 0.7–1.2 mm, margin ciliate, puberulous outside; petals spatulate to obovate, c. 2.5 by 1.2–1.5 mm, blackish crimson, pilose to glabrous; disc glands c. 0.5 mm long; stamens 3, androphore 1–1.3 mm long, anthers ellipsoid to orbicular, 0.6–0.7 mm long. *Pistillate flowers* (Chakrabarty

1984): pedicel 3.5–4 mm long, apically c. 1 mm diam, basally c. 0.5 mm diam, tomentose; sepals ovate to lanceolate, 4–6 by 1.5–2 mm, margin denticulate to entire, apex acuminate, puberulous outside, without gland or appendage; petals oblong to elliptic, c. 2 by 1–1.2 mm, blackish crimson, sparsely pilose outside; disc glands c. 0.5 mm long; ovary c. 1 mm diam, densely puberulous, stigmas c. 0.8 mm long, erect and apically bifid. *Fruits and seeds* not seen.

Distribution — India (Great Nicobar Island, endemic).

Habitat & Ecology — Primary hill forests. Flowering: May.

Notes — 1. This variety is only known from the type collection. We have only seen juvenile flowers in the specimen. The description of the staminate and pistillate flowers is based on Chakrabarty (1984).

2. This variety very closely resembles *T. villosus* Hook.f. var. *borneensis* (Merr.) Airy Shaw. The geographical distributions of the two varieties are also close (Great Nicobar Island for *T. villosus* var. *nicobaricus* and Sumatra as the western limit for *T. villosus* var. *borneensis*). The variety *nicobaricus* appears different in the somewhat longer leaf blades with an abruptly narrowed base.

30. *Trigonostemon viridissimus* (Kurz) Airy Shaw — sect.

Tylosepalum

Trigonostemon viridissimus (Kurz) Airy Shaw (1971) 545; Whitmore (1973) 135; Airy Shaw (1975) 205; (1981) 358; (1982a) 36; (1983) 48; N.P.Balakr. & Chakrab. (1991) 631, f. 12; R.I.Milne (1995) 28, in key, 29, in key; R.Y.Yu & Welzen (2018) 221. — *Sabia viridissima* Kurz (1872) 304; Hook.f. (1876) 3; Kurz (1877a) 301. — *Blachia viridissima* (Kurz) King (1896) 455, in obs. — *Kurziadendron viridissimum* (Kurz) N.P.Balakr. (1966) 68, pl. 1, f. 1–7. — Lectotype (designated here): *Kurz* s.n. (K, barcode K000246872; iso K, barcode K000246871), India, Andamans.

Neotrigonostemon diversifolius Pax & K.Hoffm. (1928) 385; (1931) 169. — Type: Parker 2593 (K), Myanmar, Mergui, Ngawun Reserve.

Trigonostemon chatterji Deb & G.K.Deka (1965) 577; N.P.Balakr. (1983) 427. — *Trigonostemon viridissimus* (Kurz) Airy Shaw var. *chatterji* (Deb & G.K.Deka) N.P.Balakr. & Chakrab. (1984c) 967, syn. nov.; (1991) 635; Talukdar et al. (2015) 10. — Type: *Deka* 19 (holo CAL (19A), barcode CAL0000023655; iso ASSAM* (19B–19E), India, Meghalaya, Jowai dist., Dawki).

Trigonostemon viridissimus (Kurz) Airy Shaw var. *confertifolius* N.P.Balakr. & N.G.Nair (1982) 36, syn. nov.; N.P.Balakr. & Chakrab. (1991) 635. — Type: Balakrishnan & Nair 4773 (holo CAL (4773A), not found; iso L (4773B), not found, PBL (4773C–4773E), not seen), India, North Andamans, Saddle Peak.

Trigonostemon huangmosu Y.T.Chang (1983) 174; H.S.Kiu (1996) 167. — Type: *Lüchun Exped.* 1961 (KUN, barcodes KUN1294366, KUN1294367), China, Yunnan, Gejju.

Shrubs or small trees, 1–10 m tall, stem up to 10 cm diam; flowering branches 1.5–3.2(–4.6) mm diam, pubescent when young, glabrescent. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts. *Bark* 0.1–0.3 mm thick, grey or pale to reddish brown or grey; wood pale yellowish, pith sometimes hollow. *Stipules* subulate to nipple-like, 0.4–1.5 mm long, caducous, often pubescent at base. *Leaves*: petiole terete but grooved above, 0.5–3.5(–5.5) cm long, 0.7–1.8 mm diam, wrinkled, pubescent when young; blade ovate to elliptic to oblong, sometimes (ob)ovate, (4.5–)8–24 by (1.5–)2.5–9 cm, membranous to chartaceous, base acute or obtuse, often with 1–2 pairs of adaxial glands, margin entire or slightly distantly serrate, apex acuminate to caudate, upper surface glabrescent to glabrous, dark green, lower surface often sparsely pubescent, paler and dull green; venation triplinerved, midrib slightly raised above and elevated beneath, often pubescent, especially near base, secondary veins 5–10 pairs, bow-shaped and connected along margin, tertiary veins scalariform, veinlets reticulate. *Inflorescences* bisexual, terminal or axillary, loose panicles; main axis terete, up to 30 cm long, 0.4–2 mm diam, slightly pubescent; bracts lanceolate, 0.5–6 by 0.2–1 mm, pubescent.

Staminate flowers 5–9 mm diam; buds conical; pedicel 4.5–9 mm long, 0.15–0.2 mm diam, glabrescent or slightly pubescent; sepals elliptic to orbicular to triangular, 1–1.7 by 0.6–1.2 mm, imbricate, margin somewhat undulate, apex rounded or truncate, sometimes with a short notch and an apical gland, pubescent outside; petals obovate, 3–6.5(–10) by 2.5–4.5(–7) mm, contort, membranous, with several distinct parallel veins, base cuneate or somewhat claw-like, entire, apex rounded, yellow to orange, glabrous; disc annular, margin undulate, reflexed, sometimes with 5 notches; stamens 3, androphore 0.7–1.5 mm long, free part of filaments 0.3–0.4(–0.6) mm long, anthers free, ellipsoid, 0.4–0.5 mm long. **Pistillate flowers** 5–9 mm diam; buds conical; pedicel slightly thickening toward apex, 0.3–1.4 cm long, apically 0.5–0.7 mm diam when flowering, elongating up to 1.1–2.9 cm long and 0.8–2 mm diam in fruit, glabrescent, often with translucent (oil?) dots; sepals, petals and disc as staminate flowers, petals caducous when fruiting; ovary 0.8–1.1 mm diam, glabrous, with numerous translucent (oil?) dots on surface, styles 0.2–0.7 mm long, stigmas 0.5–1.5 mm long, erect or bent, apically slightly thickened and slightly bifid or horseshoe-like. **Fruits** 1.1–1.5 cm diam, greenish, glabrous, smooth; sepals persistent but not accrescent; wall 0.4–0.5 mm thick, exocarp partly detaching; columella 5–6.3 mm long. **Seeds** 7–8 mm diam, with numerous translucent (oil?) dots on surface; hilum rhombic to oblong, 1.5 by 0.6–1.2 mm.

Distribution — India, Myanmar (Mergui), China, Laos, Thailand, Vietnam, Malay Peninsula, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands.

Habitat & Ecology — Primary to secondary forests, along coasts to hillsides, sometimes along rivers.

Note — The species has perhaps the widest distribution in the genus and displays a wide range of morphological variation, even within its type locality, the Andamans (India). Because the variation appears to be continuous, it was not possible to distinguish between binomials; we thus treat them as a single species.

Key to the varieties

1. Inflorescences pendulous and often pubescent, axis sympodial branching (at least at tertiary and lower branches); style distinct, up to 0.7 mm long; stigmas often erect a. var. *viridissimus*
1. Inflorescences erect and glabrous, axis monopodial; style sometimes indistinct, 0.2–0.4 mm long; stigmas bent b. var. *elegantissimus*

a. var. *viridissimus* — Map 15

Trigonostemon viridissimus (Kurz) Airy Shaw var. *viridissimus*: Airy Shaw (1975) 205.

Inflorescences pendulous and often pubescent, axis sympodial branching (at least at tertiary and lower branches). Style distinct, up to 0.7 mm long; stigmas often erect.

Distribution — India (Andamans, Assam), Myanmar (Mergui), Thailand, Malay Peninsula, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands.

Habitat & Ecology — Elevation: 0–450 m. Flowering: all year round; fruiting: January, May, July, November.

b. var. *elegantissimus* (Airy Shaw) Airy Shaw — Map 15

Trigonostemon viridissimus (Kurz) Airy Shaw var. *elegantissimus* (Airy Shaw) Airy Shaw (1975) 206; R.Y.Yu & Welzen (2018) 222. — *Trigonostemon elegantissimus* Airy Shaw (1966) 48; Whitmore (1973) 135; Airy Shaw (1978) 417; R.I.Milne (1995) 28, in key, 29, in key, 47. — Type: *Kostermans* 13695 (holo K, barcode K000959295; iso BO, sheet no. BO1722352, L, barcode L.2258606), Indonesia, E Kalimantan, Sangkulirang District, Karangan River, near Batu Pondong.

Trigonostemon chinensis Merr. (1922) 498; H.S.Kiu (1996) 167; P.T.Li et al. (2006) 118; P.T.Li & M.G.Gilbert (2008) 274, syn. nov. — Type: *Tsoong* 1875 (PE, barcode PE01110916, PNH, sheet no. 88948), China, Guangxi, Tung Sing [= Dongxing], Dongjingshan.

Trigonostemon sanguineus Gagnep. (1925a) 470. — Type: *Poilane* 8201 (P, barcodes P00717146, P00717147), Vietnam, km 26 route from Nhatrang to Ninh Hoa.

Trigonostemon kwangsiensis Hand.-Mazz. (1932) 130. — Type: *Ching* 7729 (A, barcode A00048864, NY, barcode NY00273338), China, Guangxi, Bako Schan.

Trigonostemon fungii Merr. (1932) 47. — *Trigonostemon chinensis* Merr. f. *fungii* (Merr.) Y.T.Chang (1989) 149; H.S.Kiu (1996) 169. — Type: *Tsang & Fung* 18170 (IBSC, not found), China, Hainan. — Paratype: *Tsang & Fung* 17606 (IBSC, barcodes IBSC0306872, IBSC0306873), China, Hainan, Hongmaoshan.

Trigonostemon leucanthus Airy Shaw var. *hainanensis* H.S.Kiu in H.S.Kiu & X.X.Chen (1992) 211. — Type: *Liang* 62132 (holo IBSC, barcode IBSC0306909; iso IBK, barcode IBK00169494), China, Hainan, Yazhou, Heiluoling, Xiaobaokang.

Inflorescences erect and glabrous, axis monopodial; styles distinct, up to 0.7 mm long. **Styles** sometimes indistinct, 0.2–0.4 mm long; stigmas bent.

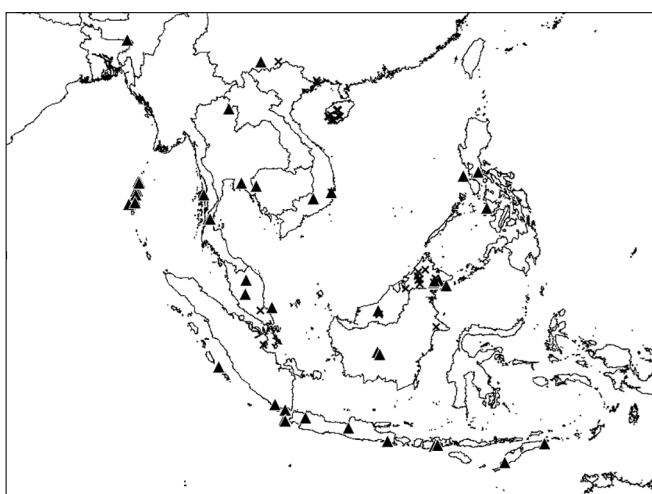
Distribution — China, Laos, Vietnam, Malay Peninsula, Borneo.

Habitat & Ecology — Growing on sandy loam to sandy stone. Elevation: 170–670 m. Flowering: March to September; fruiting: July, October.

31. *Trigonostemon xyphophylloides* (Croizat) L.K.Dai & T.L.Wu — sect. *Tylosepalum* — Fig. 4; Map 8

Trigonostemon xyphophylloides (Croizat) L.K.Dai & T.L.Wu in Chun et al. (1963) 277; H.S.Kiu (1996) 163; P.T.Li & M.G.Gilbert (2008) 273. — *Cleidion xyphophylloides* Croizat (1940) 503. — Type: *Wang* 34005 [cited as '34006' in Croizat 1940, probably a typo; marked as holotype in A by Croizat] (A*, barcode A0004596, IBK, barcode IBK00169539, IBSC, K, barcode K000959334), China, Hainan, Ya County.

Small trees, 1.5–3 m tall; flowering branches c. 3.5 mm thick, often glabrous. **Bark** 0.3–0.5 mm diam, dark brown to grey, sap reddish black when solidified; wood pale brown, pith sometimes hollow. **Stipules** subulate, 1.9–2.4 mm long, light green, glabrous or sometimes pubescent at base. **Leaves**: petiole 0.5–3 cm long, slightly grooved above, more or less pubescent; blade oblanceolate, lower part cuneately narrowed, 22–49 by 5.4–11 cm, coriaceous, base round to truncate, adaxially 2 stipellae present, subulate to falcate to linear, 1.9–2.2 by 0.3–0.6 mm, yellow to light green, blade margin distantly serrate, teeth glandular, apex acuminate or sometimes rounded, green above,



Map 15 Distribution of *Trigonostemon viridissimus* (Kurz) Airy Shaw var. *viridissimus* (▲) and *T. viridissimus* var. *elegantissimus* (Airy Shaw) Airy Shaw (✖).



Fig. 4 *Trigonostemon xyphophyloides* (Croizat) L.K.Dai & T.L.Wu, cultivated in South China Botanical Garden. a. Growing habit; b. leaf base, showing stipule; c. branch tip, showing stipules; d. bark; e. branch, showing ramiflorous inflorescences; f. top view of staminate flower; g. flower buds and lateral view of staminate flowers; h. columella of fruit. — Photos by Ren-Yong Yu.

light green beneath, glabrous on both surfaces; venation pinnate, midrib slightly raised above, distinctly elevated beneath, secondary veins 13–18 pairs, slightly curved, bifurcate and connected near margin, tertiary veins reticulate. Inflorescences unisexual; staminate ones cauliflorous, short and condensed cymes or thyrses, bracts semi-orbicular to lanceolate, 0.3–1.8 by 0.3–1.5 mm, pubescent; pistillate ones terminal or axillary, often racemose, axis 1.5–2.4 cm long, pubescent, bracts lanceolate, 1.3–2.4 by 0.8–1 mm, pubescent. Staminate flowers 3.1–4 mm diam; pedicel 3.1–6 mm long, 0.1–0.2 mm diam, pinkish, glabrous; sepals ovate to elliptic, 1–1.2 by 0.7–1 mm, imbricate, pinkish green, base connate, apex often rounded, more or less pubescent outside, sometimes with an apical gland outside; petals oblong to oblanceolate, 1.5–5.3 by 0.5–1.3 mm, orange with a reddish honey mark at base, visible on both sides, apex acute, glabrous on both sides; disc glands rectangular to trapezoid, 0.25–0.35 by 0.25–0.4 mm, somewhat fleshy, apex

truncate to rounded; stamens 3, androphore erect, 0.2–0.3 mm long, c. 0.3 mm diam, anthers free, divaricate, thecae 0.4–0.5 mm long, connective with an apical appendage. Pistillate flowers (bud) at least 2 mm diam; pedicel c. 3 mm long, c. 0.5 mm diam, pubescent; sepals ovate to triangular, c. 1 by 0.9 mm, pubescent; petals, disc and ovary not seen. Fruits green, glabrous; pedicel 0.8–1 cm long, c. 2.8 mm diam; sepals persistent, slightly accrescent, c. 2 by 1.2 mm; columella 6.5–8 mm long. Seeds globose or ellipsoid, 0.85–0.9 by 0.7–0.85 mm, dark orange to brown when dry.

Distribution — China (Hainan, endemic?).

Habitat & Ecology — Understorey in forests. Flowering: July; fruiting: April, July, September to October.

Note — The species is both morphologically and phylogenetically (Yu et al. 2019) close to *T. aurantiacus*, but the leaves are much larger and lighter in colour.

DOUBTFUL SPECIES

32. *Trigonostemon praetervisus* Airy Shaw — Map 6

Trigonostemon praetervisus Airy Shaw (1982b) 121; N.P. Balakr. & Chakrab. (1991) 625. — Type: *Wallich 8001* (holo K, part of the specimen, as it shares the same sheet with *Croton chlorocalyx* Müll.Arg., barcode K000246858), Bangladesh, Assam, Sylhet.

No material was available, for description see Airy Shaw (1982b).

Note — The species was described based on incomplete material. There are two sheets of *Wallich 8001* in Kew: barcodes K000246857 and K000246858. On the first sheet, a drawing shows 10 fully separate stamens (10 separate filaments can be clearly seen), which is atypical for *Trigonostemon*; on the second sheet, there is a mixed assemblage of, as Airy Shaw (1982b) described, *Croton chlorocalyx* and *Trigonostemon praetervisus*. However, we were unable to designate a genus to the material. Therefore, the species is treated as doubtful here.

EXCLUDED NAMES

Trigonostemon beddomei (Benth.) N.P.Balakr. (1968) 245 = *Tritaxis beddomei* Benth. (1878) 221. — *Dimorphocalyx beddomei* (Benth.) Airy Shaw (1969) 124. — Type: *Beddome 37* (K, barcode K000246899), India, East-Indian Peninsula, Tinnevelly (Yu et al. 2019).

Trigonostemon cumingii Müll.Arg. (1865) 213; (1866) 1107; Yu & Welzen (2018) 224. = *Tritaxis cumingii* (Müll.Arg.) Benth. (1878) 221; Pax (1910) 114; Merr. (1923) 449. — *Dimorphocalyx cumingii* (Müll.Arg.) Airy Shaw (1969) 124; (1983) 20. — Type: *Cuming 1693* (G-DC*, barcode G00319795; isotypes: BM, barcodes BM000951496, BM000951497, E*, barcode E00570192, G*, barcode G00435094, K, barcodes K000959395, K000959396, L, barcodes L 0016166, L 0016167, P, barcode P00640260), Philippines, Samar (Yu et al. 2019).

Trigonostemon gaudichaudii (Baill.) Müll.Arg. (1865) 213 = *Tritaxis gaudichaudii* Baill. (1858a) 343; Müll.Arg. (1865) 213; (1866) 1107; Pax & K.Hoffm. (1911) 94; Gagnep. (1925b) 302; Pax & K.Hoffm. in Engl. & Prantl (1931) 167. — Lectotype (designated by Yu et al. 2019): *Gaudichaud 278* (P, barcode P00712262; iso P, barcodes P00712260, P00712261), Vietnam (Yu et al. 2019).

Trigonostemon lawianus (Nimmo) Müll.Arg. (1865) 212; (1866) 1105 = *Tritaxis glabella* (Thwaites) R.Y.Yu & Welzen var. *lawiana* (Nimmo) R.Y.Yu & Welzen in Yu et al. (2019) 932. — *Croton lawianus* Nimmo (1839) 251; Dalzell & A.Gibson (1861) 232. — *Dimorphocalyx lawianus* (Nimmo) Hook.f. (1887) 404. — *Dimorphocalyx glabellus* Thwaites var. *lawianus* (Nimmo) Chakrab. & N.P.Balakr. (1990) 296. — Type: *Gibson 19* (K, barcode K000246856), India, Bombay, Bheema Snaker (Yu et al. 2019).

Trigonostemon voratus Croizat (1942) 52 = *Vavaea megaphylla* C.H.Wright (1895) 102 [Meliaceae]. — Type: *Tabualewa 15569* (holo A*, barcode A00105962; iso BISH*, barcode BISH1003379, K, barcode K000651877, NY*, barcode NY00273356, US*, barcode US00096545), Fiji, Viti Levu, Tholo West, Mbuyombuyo, near Xamboutini (Smith 1952, Pennington 1969).

Trigonostemon zeylanicus (Müll.Arg.) Müll.Arg. (1865) 213 = *Paracroton zeylanicus* (Müll.Arg.) N.P.Balakr. & Chakrab. (1993) 723. — *Tritaxis zeylanica* Müll.Arg. (1864a) 482. — Type: not designated, cultivated in garden (Balakrishnan & Chakrabarty 1993).

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IDENTIFICATION LIST

The list includes all herbarium specimens of *Trigonostemon* species seen by us.

1 =	<i>T. adenocalyx</i> Gagnep.	24 =	<i>T. lanceolatus</i> (S.Moore) Pax	50a =	<i>T. verticillatus</i> (Jack) Pax var. <i>verticillatus</i>
2 =	<i>T. apetalogyne</i> Airy Shaw	25 =	<i>T. lii</i> Y.T.Chang	50b =	<i>T. verticillatus</i> (Jack) Pax var. <i>salicifolius</i> (Ridl.) Whitmore
3 =	<i>T. aurantiacus</i> (Kurz ex Teijsm. & Binn.) Boerl.	26 =	<i>T. longifolius</i> Baill.	51 =	<i>T. victoriae</i> R.Y.Yu & Welzen
4 =	<i>T. balgooyi</i> R.Y.Yu & Welzen	27 =	<i>T. longipes</i> (Merr.) Merr.	52a =	<i>T. villosus</i> Hook.f. var. <i>villosus</i>
5 =	<i>T. beccarii</i> Ridl.	28 =	<i>T. lychnos</i> (R.I.Milne) R.Y.Yu & Welzen	52b =	<i>T. villosus</i> Hook.f. var. <i>borneensis</i> (Merr.) Airy Shaw
6 =	<i>T. bonianus</i> Gagnep.	29 =	<i>T. magnificus</i> R.I.Milne	52c =	<i>T. villosus</i> Hook.f. var. <i>cordatus</i> R.Y.Yu & Welzen
7 =	<i>T. calciculus</i> (R.I.Milne) R.Y.Yu & Welzen	30 =	<i>T. malaccanus</i> Müll.Arg.	52d =	<i>T. villosus</i> Hook.f. var. <i>merrillianus</i> (Airy Shaw) R.Y.Yu & Welzen
8 =	<i>T. capillipes</i> (Hook.f.) Airy Shaw	31 =	<i>T. merrillii</i> Elmer	52e =	<i>T. villosus</i> Hook.f. var. <i>nicobaricus</i> (Chakrab.) N.P.Balakr. & Chakrab.
9 =	<i>T. capitellatus</i> Gagnep.	32 =	<i>T. montanus</i> R.Y.Yu & Welzen	53a =	<i>T. viridissimus</i> (Kurz) Airy Shaw var. <i>viridissimus</i>
10 =	<i>T. cherrieri</i> Veillon	33 =	<i>T. murtonii</i> Craib	53b =	<i>T. viridissimus</i> (Kurz) Airy Shaw var. <i>elegantissimus</i> (Airy Shaw)
11 =	<i>T. detritiferus</i> R.I.Milne	34 =	<i>T. nemoralis</i> Thwaites	54 =	<i>T. wetriifolius</i> Airy Shaw & Ng
12 =	<i>T. diffusus</i> Merr.	35 =	<i>T. oblongifolius</i> Merr.	55 =	<i>T. wildeorum</i> R.Y.Yu & Welzen
13 =	<i>T. diplopetalus</i> Thwaites	36 =	<i>T. pachyphyllus</i> Airy Shaw	56 =	<i>T. xyphophylloides</i> (Croizat) L.K.Dai & T.L.Wu
14 =	<i>T. dipteranthus</i> Airy Shaw	37 =	<i>T. palustris</i> R.Y.Yu & Welzen	doubtful 57 =	<i>T. angustifolius</i> Merr.
15 =	<i>T. eberhardtii</i> Gagnep.	38 =	<i>T. pentandrus</i> Pax & K.Hoffm.	doubtful 58 =	<i>T. praeteritus</i> Airy Shaw
16 =	<i>T. filiformis</i> Quisumb.	39 =	<i>T. philippinensis</i> Stapf	doubtful 59 =	<i>T. whiteanus</i> (Croizat) Airy Shaw
17 =	<i>T. flavidus</i> Gagnep.	40 =	<i>T. polyanthus</i> Merr.		
18 =	<i>T. fragilis</i> (Gagnep.) Airy Shaw	41 =	<i>T. quocensis</i> Gagnep.		
19 =	<i>T. hartleyi</i> Airy Shaw	42 =	<i>T. reidioides</i> (Kurz) Craib		
20 =	<i>T. heteranthus</i> Wight	43 =	<i>T. rufescens</i> Jabl.		
21 =	<i>T. inopinatus</i> Airy Shaw	44 =	<i>T. sandakanensis</i> Jabl.		
22 =	<i>T. kerrii</i> Craib	45 =	<i>T. scopulatus</i> R.Y.Yu & Welzen		
23a =	<i>T. laevigatus</i> Müll.Arg. var. <i>laevigatus</i> (B.C.Stone) R.Y.Yu & Welzen	46 =	<i>T. semperflorens</i> (Roxb.) Müll.Arg.		
23b =	<i>T. laevigatus</i> Müll.Arg. var. <i>croceus</i>	47 =	<i>T. serratus</i> Blume		
		48 =	<i>T. sinclairii</i> Jabl.		
		49 =	<i>T. tuberculatus</i> F.Du & Ju He		

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