A taxonomic revision of Trigonostemon (Euphorbiaceae) in Malesia

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Key words

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Abstract Trigonostemon is taxonomically revised for Malesia based on herbarium collections and field observations. Thirty-eight species are recognized in Malesia, of which four of uncertain status and four newly described. The previous infrageneric classifications are briefly reviewed, but none is accepted. Some useful characters are discussed. An identification key, nomenclature, descriptions, typification, geographic distributions and taxonomic notes are provided.

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INTRODUCTION

Trigonostemon Blume is a genus in the Euphorbiaceae subfamily Crotonoideae (phylogenetically supported based on molecular data by Wurdack et al. 2005). Within the Crotonoideae it is traditionally classified in tribe Trigonostemoneae (Webster 1975, 1994, Radcliffe-Smith 2001) or tribe Codiaeae subtribe Trigonostemoniae (Webster 2014), but none of these treatments has been confirmed by a molecular phylogeny. The genus contains about 60 species ranging from India to China, throughout mainland SE Asia and Malesia to NE Australia and the W Pacific (Govaerts et al. 2000). There are 38 species in Malesia based on this revision.

Jack (1822) described the first taxon, the genus Enchidium Jack based on the Sumatran E. verticillatum Jack as the type. However, Jack cited a wrong illustration for E. verticillatum (Rumphius 1743: t. 106, see Merrill 1952) and the genus remained monotypic ever since the publication. Because of the obscure status of Enchidium and the wide use of the name Trigonostemon, Van Steenis (1948, 1953) proposed to reject the genus name *Enchidium* in favour of *Trigonostemon*, which was adopted by the Eighth International Botanical Congress (see The General Committee and Advisory Board 1954; The Nomenclature section of the VIIIth International Botanical Congress, Paris 1954).

Trigonostemon was described by Blume in 1825 (as 'Trigostemon', corrected in 1828) on the basis of the three connate stamens, with as type *T. serratus* Blume. More than 140 scientific names were published within the genus Trigonostemon over the years.

Besides Trignonostemon, a few other plant genera with connate stamens in the Euphorbiaceae were described, for example, the two Indian genera Silvaea Hook. & Arn. (Hooker & Arnott 1837; 3 connate stamens) and Athroisma Griff. (Griffith 1854a, b; 3 connate stamens). Baillon (1858) adopted them as genera distinct from Trigonostemon and proposed his own genera Telogyne Baill. (5 connate stamens) and Tritaxis Baill. (3 whorls of stamens, only the inner 2 whorls connate). Later, two other genera, Dimorphocalyx Thwaites (1861; staminate flowers with 2 whorls of stamens, only the inner whorl connate) and Tylosepalum Kurz ex Teijsm. & Binn. (Teijsmann & Binnendijk 1864; 3 connate stamens and a gland on the sepals), were described. All of them were morphologically rather similar and this triggered a discussion about the circumscription and infrageneric classification of Trigonostemon.

Müller Argoviensis (1865, 1866) considered Trigonostemon in a wide sense, a genus that did not only include species with one whorl of 3 or 5 connate stamens, as Blume (1825) defined it, but also those with 2 or 3 whorls of (partly) free stamens. He divided the genus into 7 sections (the type of each section is in **bolditalic**):

- Sect. 1. Dimorphocalyx (Thwaites) Müll.Arg. (former Dimorphocalyx Thwaites; comprising the type D. glabellus as a synonym of T. lawianus (Nimmo ex Dalzell & A.Gibson) Müll.Arg.); nowadays considered as a distinct genus:
- Sect. 2. Cheilosopsis Müll.Arg. (newly proposed section, comprising T. macrophyllus (Müll.Arg.) Müll.Arg. and T. zeylanicus (Müll.Arg.) Müll.Arg., no type designated between the two of them, but these two species were respectively transferred to Paracroton Miq. by Esser (2007) and by Balakrishnan & Chakrabarty (1993));
- Sect. 3. Tritaxis (Baill.) Müll.Arg. (former Tritaxis; comprising *Trig. gaudichaudii* (Baill.) Müll.Arg.);
- Sect. 4. Anisotaxis Müll.Arg. (newly proposed section with 2 whorls of stamens; type T. cumingii Müll.Arg.);
- Sect. 5. Telogyne (Baill.) Müll.Arg. (former Telogyne Baill.; comprising *Trig. indicus* (Baill.) Müll.Arg.);
- Sect. 6. Eutrigonostemon Müll.Arg. (invalid name, autonym for the genus is required, as it contains the type species; comprising *T. diplopetalus* Thwaites, *T. heteranthus* Wight, T. hookerianus (Baill.) Müll.Arg., T. laetus Baill. ex Müll.Arg., T. longifolius Wall. ex Müll.Arg., T. nemoralis Thwaites, T. serratus);
- Sect. 7. Silvaea (Hook. & Arn.) Müll.Arg. (former Silvaea Hook. & Arn.; comprising T. laevigatus Müll.Arg., T. malaccanus Müll.Arg., T. semperflorens (Roxb.) Müll.Arg.).

Müller Argoviensis (1866) also downgraded Tylosepalum to a section under Codiaeum Rumph. ex A.Juss.

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Opposed to Müller Argoviensis (1865, 1866), Bentham (1878, 1880) and Hooker (1887) regarded the genus *Trigonostemon* to consist only of species with one whorl of connate stamens (comparable to sections 5-7 of Müller Argoviensis 1865, 1866). They combined Müller Argoviensis's sect. Silvaea into sect. Eutrigonostemon and raised group §1 (T. diplopetalus and T. nemoralis) of Müller Argoviensis's sect. Eutrigonostemon to the new sect. Pycnanthera Benth. (no type species designated). Bentham (1880) tended to exclude T. laevigatus from Trigonostemon since it has petals in the pistillate flowers, whereas other species were thought not to have these (however, actually the petals in pistillate flowers are present but often early caducous). He also pointed out that Tylosepalum is more likely to be part of *Trigonostemon*, but he did not formally arrange this. Bentham (1878, 1880) and Hooker (1887) changed the infragenetic classification (the type of each section is in **bolditalic**):

- Sect. 1. Eutrigonostemon (T. heteranthus, T. laetus, T. longifolius, T. malaccanus, T. semperflorens (including T. hookerianus), T. serratus, T. villosus Hook.f.);
- Sect. 2. Telogyne (Trig. indicus);
- Sect. 3. *Pycnanthera* (*T. diplopetalus* (lectotype designated here), *T. nemoralis*).

Pax (1890) adopted Bentham's (1878, 1880) and Hooker's (1887) system, but he and Hoffmann (Pax & Hoffmann 1911) reduced *Tylosepalum* to a fourth section of *Trigonostemon*. Merrill (1924) proposed a new sect. *Dichotomae* Merr. based on *T. petelotii* Merr., which was also adopted by Pax & Hoffmann (1931). Pax and Hoffmann's system (Pax 1890, Pax & Hoffmann 1911, 1912a, b, 1914, 1919, 1931) was (the type of each section is in *bolditalic*):

- Sect. 1. Telogyne (Trig. pentandrus Pax & K.Hoffm., Trig. verticillatus (Jack) Pax (including Tr. indicus));
- Sect. 2. Eutrigonostemon (T. forbesii Pax, T. heteranthus, T. hirsutus C.B.Rob., T. laetus, T. longifolius, T. malaccanus, T. merrillii Elmer, T. murtonii Craib, T. oblanceolatus C.B.Rob., T. oblongifolius Merr., T. ovatifolius J.J.Sm. (including T. membranaceus Pax & K.Hoffm.), T. philippinensis Stapf, T. semperflorens (including T. hookerianus), T. serratus, T. sumatrus Pax & K.Hoffm., T. thyrsoideus Stapf, T. tomentellus Pax & K.Hoffm., T. villosus, T. wenzelii Merr.);
- Sect. 3. Dichotomae (T. petelotii);
- Sect. 4. *Pycnanthera* (*T. diplopetalus* (lectotype designated here), *T. lanceolatus* (S.Moore) Pax, *T. nemoralis*);
- Sect. 5. *Tylosepalum* Pax & K.Hoffm. (*Trig. aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl.);
- species of uncertain position (*T. acuminatus* Merr., *T. laevigatus*, *T. longipedunculatus* (Elmer) Elmer, *T. longipes* (Merr.) Merr., *T. oliganthus* K.Schum., *T. reidioides* (Kurz) Craib).

Airy Shaw (1969, 1972a) had an eclectic opinion on the delimitation of the genus as compared to the previous authors. Like Bentham and Hooker (Bentham 1878, 1880, Hooker 1887) and Pax and Hoffmann's systems (Pax 1890, Pax & Hoffmann 1911, 1912a, b, 1914, 1919, 1931), he treated the genus *Trigonostemon* separate from *Dimorphocalyx*, by a combination of character states, even though the character states separately showed overlap between the genera. He indicated that *Trigonostemon* more frequently has triplinerved leaves, is always monoecious and has coloured flowers (usually dioecious and white in *Dimorphocalyx*), 3 or 5 stamens united into 1 whorl (2 whorls in *Dimorphocalyx* in which the outer one with more or less free stamens) and less frequently accrescent pistillate sepals in fruits. However, he oddly adopted Müller Argoviensis's (1865, 1866) treatment of the genus *Tritaxis* and included

Trit. gaudichaudii Baill., a species of 3 whorls of stamens (13 stamens as he described in the identification key; Airy Shaw 1969), in *Trigonostemon*, making it a species obviously aberrant among all others. Recently, Van Welzen & Van Oostrum (2015), in their revision of the Malesian *Dimorphocalyx* tended to regard *Dimorphocalyx* as a group with 3 whorls of stamens. Focusing on the Malesian region, Jablonski (1963) made a revision of the *Trigonostemon* species from the Malay Peninsula, Sumatra and Borneo, in which he recorded 26 species, but only 12 species are based on complete material and very few of them have adequate descriptions. He used the differences in stigmas and anthers to classify the genus into 3 sections (* refers to inadequately known species):

- Sect. 1. Telogyne (stigmas deeply bifid, connectives without an appendage): Trig. arboreus Ridl.*, Trig. beccarii Ridl.*, Trig. indicus, Trig. longisepalus Ridl.*, Trig. malaccanus, Trig. pentadrus*, Trig. salicifolius Ridl., Trig. sinclairii Jabl., Trig. rufescens Jabl., Trig. verticillatus*, Trig. villosus, Trigonostemon sp. nov., aff. indicus* (Perlis), Trigonostemon sp. nov., aff. indicus* (Thailand), Trigonostemon sp. nov., aff. malaccanus* (Siberut), Trigonostemon sp. nov., aff. malaccanus* (Sumatra).
- Sect. 2. *Trigonostemon* (stigmas entire or slightly bifid, connectives with an appendage): *T. borneensis* Merr., *T. elmeri* Merr., *T. forbesii**, *T. laevigatus**, *T. longifolius*, *T. ridleyi* Jabl.*, *T. sandakanensis* Jabl., *T. sumatrus*.
- Sect. 3. *Tylosepalum* (stigmas entire or slightly bifid, connectives without an appendage): *Trig. diffusus*, *Trigonostemon* sp. nov., aff. *chinensis** (Anambas), *Trigonostemon* sp. nov., aff. *chinensis** (Pahang).

Revisions in local floras or checklists added extra species: Malay Peninsula (Whitmore 1973), Sumatra (Airy Shaw 1981), Java (Backer & Bakhuizen van den Brink Jr 1963), Borneo (Airy Shaw 1975), Philippines (Airy Shaw 1983b), Sulawesi, Moluccas and Lesser Sunda Islands (Airy Shaw 1982), New Guinea (Airy Shaw 1980b). Most of these contributions lack proper descriptions. Milne (1994, 1995a, b) revised the genus, but merely described new entities and he provided a key to the Bornean species only (Milne 1995a).

Being morphologically variable (see Characters below) and closely resembling a few other genera (e.g., Dimorphocalyx, Tritaxis, Ostodes), Trigonostemon is a difficult genus to define and classify, and any circumscription and infrageneric classification based on only morphological characters may be arbitrary and unnatural. It will not be until the phylogeny of *Trigonostemon* is resolved and the clades are identified, that an infrageneric classification becomes feasible and desirable. Therefore, the present treatment uses no infrageneric classification. The aim of this study is to give a comprehensive revision of the Malesian Trigonostemon species, which will be the basis for an accurate molecular phylogeny and will also contribute as a precursor to Flora Malesiana, with an identification key, nomenclature, typification, geographic distributions and local names based on herbarium collections. The genus concept adopted here is more or less according to Blume's strict sense (Blume 1825) of species with one whorl of 3 or 5 united stamens. Species boundaries based on distinct morphological discontinuities are proposed and applied in this revision.

Characters

The morphology of *Trigonostemon* is discussed below. Possible useful characters in species identifications and subgeneric classification are pointed out. A subgeneric taxonomy will be presented in our future publications based on palynological, anatomical and molecular phylogenetic data.

Indumentum

The hairs are always simple with two exceptions, stellately bundled simple hairs are found in *T. balgooyi* R.Y.Yu & Welzen and *T. reidioides* (Kurz) Craib (only present in Thailand and Indochina). The young parts, branchlets and buds are always densely hairy, and to a different degree hairy in the older parts. The indumentum sometimes shows characters typical for particular species, e.g., *T. merrillii* differs from *T. oblongifolius* in the densely hairy upper surface of the leaf blades, and *T. rufescens* and *T. sinclairii* are both distinct because of their extremely dense indumentum.

In most cases the hairs show a single length, but in some species hairs of two different lengths are present (e.g., sepals of *T. laevigatus*, branchlets, leaves and inflorescences of *T. sinclairii* and *T. balgooyi*). The hairs vary from whitish to golden yellowish, from short to long and from soft silky to stiff hispid and sometimes they have a somewhat bulbose base.

Leaf morphology

Petioles and blades are variable in shape and size among the species and even within species (e.g., *T. villosus*). When using dried specimens, *T. oblongifolius* is unusual because of the paler upper surface of the leaf blades (while other species are always paler on the lower surface). *Trigonostemon verticillatus* and *T. viridissimus* (Kurz) Airy Shaw can be recognized by the occasional presence of 2 (or even more) pairs of glands on the upper leaf base (whereas other species only have 1 pair).

The venation is pinnate, but several species, mainly those with an appendage on the connective (discussed below) are triplinerved. However, in many specimens the two basal veins are only slightly stronger without a different angle to the midrib, which makes the use of this character, generally thought to be distinctive, difficult. The venation is treated as triplinerved if the basal veins are discernibly thicker than the others.

Inflorescences

The inflorescences come in various forms and are sometimes helpful in species delimitation. *Trigonostemon polyanthus* Merr. is easily separated from the *T. villosus* species complex by its paintbrush-like inflorescences, and *T. diffusus* and *T. magnificus* R.I.Milne are characterized by their inflorescences being extremely branched and developed. Sometimes flowers being cauliflorous can be taxonomically significant, for example, *T. wildeorum* closely resembles *T. aurantiacus* but differs from the latter by its pistillate flowers being always cauliflorous. Bracts are often insignificant. They are single per flower and node, but in *T. dipteranthus* and *T. lychnos*, the glomerules are subtended by two or more showy leaf-like bracts.

Dichogamy is present in many species and species may appear to be dioecious. Milne (1995a) pointed out that the inflorescences always develop with the potential to combine staminate and pistillate flowers. The sexuality of inflorescences is not a fixed character, often among staminate flowers a few pistillate ones are present. For that reason, *T. thyrsoideus* is synonymised with *T. philippinensis*.

Flowers

The pedicel of staminate flowers is usually more slender and glabrous than that of pistillate flowers, which is thicker, more hairy, often thickened towards the apex and sometimes elongating when fruiting.

The sepals show differences between staminate and pistillate flowers. The pistillate sepals are sometimes accrescent in fruit and tend to be larger and more hairy outside than the staminate sepals. The pistillate sepals are usually persistent. Some spe-

cies have sepals with a subapical gland outside and this was used as typical character to recognize the genus *Tylosepalum* (Teijsmann & Binnendijk 1864), and the later sect. *Tylosepalum* (Pax & Hoffmann 1911). However, unlike in the genus *Dimorphocalyx*, the presence of glands in *Trigonostemon* is not always stable within a species and sometimes the glands can be very faint and indiscernible or showy or even protruding, e.g., *T. laevigatus*. Therefore, it is not used here to delimit species.

The petals of *Trigonostemon* are often identical in staminate and pistillate flowers. They are of various colours (white, yellow, orange, pink, red, purple, etc.) and in some species a light flame-like honey mark is often basally present in the middle. The petals are always glabrous and smooth outside but sometimes rough and scabrous (probably some glandular tissue) inside, which is often only seen in mature flowers.

The disc shape in pistillate flowers is more or less correlated with that of the staminate flowers. If the disc in staminate flowers is annular, then it is also annular in pistillate flowers; if glandular in staminate ones, then variable, glandular or annular, in pistillate ones.

There are 3 or 5 connate stamens per flower and the number is stable per species. Each anther has 2 thecae and the anthers are always gathered at the top of the androphore when young. The anthers are generally sessile, directly attached to the androphore, but in some species a free filamental part is present between androphore and anthers. Since the thecae juxtapose and adhere to each other tightly, each theca just looks like a single anther, so that sometimes the plants are misperceived as having 6 or 10 anthers (e.g., Jack 1822). In most species, when the flower is mature, the anthers often divaricate at the top (except in a few species including *T. apetalogyne* Airy Shaw, T. laevigatus Müll.Arg. and T. viridissimus, and the connectives show a tendency to produce red droplets or dark reddish expanded cells as a protruding apical appendage. The presence or absence of an appendage on the connective was used by Jablonski (1963) to differentiate between sect. *Trigonostemon* and sect. Tylosepalum, respectively. Studies on pollen morphology of Trigonostemon (unpublished data) showed that two major types of pollen grains, differing in tectum ornamentation, correlate well with the presence or absence of apical anther divarication. Therefore, the divergence of the anthers forms a good character to use in a future subgeneric classification, but this should be based on mature stamens as the divergence is not visible in young stages of the anthers.

The ovary in most species is either glabrous or variably hairy, but there are a few exceptions, e.g., in *T. villosus* and *T. detritiferus* R.I.Milne, the ovaries can be both glabrous and variably hairy. Milne (1994) in his description of *T. detritiferus* attributed this to the development of ovaries. The ovary in some species (e.g., *T. longifolius*, *T. philippinensis* and *T. capitellatus* Gagnep.) is more or less warty, and this character often remains in fruits. The stigmas either completely split or are apically only very shallowly cleft. This is also congruent with the two pollen types and might also be a useful character in a possible future subgeneric taxonomy.

Fruits and seeds

Fruits and seeds in this genus are of relatively little taxonomic value, because they usually have similar shapes and structures among the species. The warty surface of the fruits is sometimes useful to identify some species. The wall thickness was measured in the middle part of the cocci, because the wall always tends to be thicker towards the apex and thinner towards the bottom of the fruits.

The seeds are ellipsoid to ovoid, smooth and ecarunculate. The seed coat is usually brownish and slightly and irregularly

thickened, forming the typical dark brownish marbled pattern. A ridge is often present around the seed in the middle and sometimes slightly thickened into a beak at apex and bottom. The sides with the hilum are often flattened and become 2 shallow fossettes. The hilum is often rhombic to heart-shaped with vascular bundle remnants in the middle and epidermal cells around are often torn off when the seeds fall off.

Taxonomy³

Trigonostemon Blume

Trigonostemon Blume (1825) 600 ('*Trigostemon*'); (1828) Preface 8 (name corrected in note), nom. cons.; Baill. (1858) 340, pl. 11, f. 12; Müll.Arg. (1865) 212; (1866) 1105; Benth. (1880) 298; Hook.f. (1887) 395; Pax (1890) 84; Pax & K.Hoffm. (1911) 85; Ridl. (1924) 263; Merr. (1923) 451; Gagnep. (1925b) 309; Pax & K.Hoffm. (1931) 169; Jabl. (1963) 151; Backer & Bakh.f. (1963) 495; Airy Shaw (1972a) 344; Whitmore (1973) 134; Airy Shaw (1975) 201; (1978) 415; (1980a) 690; (1980b) 205; (1981) 352; (1982) 36; (1983b) 46; G.L.Webster (1994) 108; R.I.Milne (1994) 445; (1995a) 25; (1995b) 51; H.S.Kiu (1996) 162; Philcox (1997) 110; Radcl.-Sm. (2001) 307; Chantar. (2005) 21; (2007) 573; P.T.Li & M.G.Gilbert (2008) 272; G.L.Webster (2014) 171. — *Trigonostemon* Blume sect. *Eutrigonostemon* Müll.Arg. (1865) 214, nom. inval.; (1866) 1108; Benth. (1878) 224; (1880) 298; Hook.f. (1887) 396; Pax (1890) 84; Pax & K.Hoffm (1911) 88; (1931) 169. — *Trigonostemon serratus* Blume.

Enchidium Jack (1822) 89, nom. rej.; Baill. (1858) 652; Müll.Arg. (1866) 1256 ('Enchidion'); Merr. (1952) 224. — Type: Enchidium verticillatum Jack (= Trigonostemon verticillatus (Jack) Pax).

Silvaea Hook. & Arn. (1837) 211, non Phil. (1860) 21, nec Meisn. (1864) 84; Baill. (1858) 341. — *Trigonostemon* Blume sect. *Silvaea* (Hook. & Arn.) Müll.Arg. (1865) 214; (1866) 1110. — Type: *Silvaea semperflorens* (Roxb.) Hook. & Arn. (= *Trigonostemon semperflorens* (Roxb.) Müll.Arg.).

Athroisma Griff. (1854) 477, nom. inval., non DC. (1833) 516. — Syntypes: Athroisma dentatum Griff. (=? Trigonostemon longifolius Wall. ex Müll. Arg.; see Hook.f. 1887: 396; Pax & Hoffmann 1911: 88), A. serratum Griff. (=? Trigonostemon heteranthus Wight; see Hook.f. 1887: 396; Pax & Hoffmann 1911: 91; =? Trigonostemon longifolius Wall. ex Müll.Arg.; see Airy Shaw 1972a: 347).

Telogyne Baill. (1858) 327, pl. 11, f. 13. — *Trigonostemon* Blume sect. *Telogyne* (Baill.) Müll.Arg. (1865) 214; (1866) 1107; Benth. (1878) 225; (1880) 298; Hook.f. (1887) 398; Pax (1890) 84; Pax & K.Hoffm. (1931) 169; Jabl. (1963) 152. — Type: *Telogyne indica* Baill. (= *Trigonostemon verticillatus* (Jack) Pax)

Tylosepalum Kurz ex Teijsm. & Binn. (1864) 50. — Codiaeum A.Juss. sect. Tylosepalum (Kurz ex Teijsm. & Binn.) Müll.Arg. (1866) 1117. — Trigonostemon Blume sect. Tylosepalum (Kurz ex Teijsm. & Binn.) Pax & K.Hoffm. (1931) 169; Jabl. (1963) 163. — Type: Tylosepalum aurantiacum Kurz ex Teijsm. & Binn. (= Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl.). Trigonostemon Blume sect. Pycnanthera Benth. (1878) 244; (1880) 299; Hook.f. (1887) 398; Pax (1890) 84; Pax & K.Hoffm. (1911) 92; (1931) 169.

— Lectotype (designated here): *Trigonostemon diplopetalus* Thwaites. *Nepenthandra* S.Moore (1905) 149. — Type: *Nepenthandra lanceolata* S.Moore (= *Trigonostemon lanceolatus* (S.Moore) Pax).

Actephilopsis Ridl. (1923) 360. — Type: Actephilopsis malayana (= Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl.).

Trigonostemon Blume sect. Dichotomae Merr. (1924) 425; Pax & K.Hoffm. (1931) 169. — Type: Trigonostemon petelotii Merr. (= Trigonostemon laevigatus Müll.Arg.).

Prosartema Gagnep. (1924) 875; (1925b) 304. — Type: Prosartema stellaris Gagnep. (= Trigonostemon stellaris (Gagnep.) Airy Shaw).

Poilaniella Gagnep. (1925a) 467; (1925b) 307. — Type: Poilaniella fragilis (= Trigonostemon fragilis (Gagnep.) Airy Shaw).

Neotrigonostemon Pax & K.Hoffm. (1928) 385; (1931) 169. — Type: Neotrigonostemon diversifolius Pax & K.Hoffm. (= Trigonostemon viridissimus (Kurz) Airy Shaw).

Kurziodendron N.P.Balakr. (1966) 68. — Type: Kurziodendron viridissimum (Kurz) N.P.Balakr. (= Trigonostemon viridissimus (Kurz) Airy Shaw).

Shrubs to trees, monoecious; branches terete, often with leaf scars, rarely with adventitious roots (*T. detritiferus*, *T. wetriifolius*

Airy Shaw & Ng and T. sandakanensis Jabl.); branches often hollow; buds densely hairy. Indumentum of simple hairs (T. balgooyi and T. reidioides also stellately bundled hairs), dense on young parts. Bark often containing sticky, translucent to orange, pinkish or reddish sap. Stipules 2, small, caducous. Leaves simple, alternate, sometimes clustered near branch tips; petiole often flat or grooved above and rounded below; blade variable in shape and size, occasionally slightly asymmetric, often with 1 pair (2 pairs in *T. verticillatus* and *T. viridissimus*) of glands at base above, margin entire or laxly serrate to crenate, teeth often small, glandular (nipple-like) to falcate, both sides greenish, glabrous to hairy, often paler (except in T. oblongifolius) and more hairy on lower side; venation pinnate or triplinerved, often more or less elevated on both sides, more so below, secondary nerves often curved and connected along margin, tertiary veins sometimes scalariform, higher order veins reticulate. Inflorescences unisexual or bisexual, axillary or terminal, sometimes cauline, often thyrsoid or paniculate, sometimes reduced and cymose or racemose (especially pistillate ones), staminate flowers often clustered into short cymes, pistillate flowers often single on each node; bracts of various shapes, sometimes leaf-like. Staminate flowers less than 1 cm diam; pedicel often slender; sepals 5, imbricate when young, connate at base, outer surface often hairy, sometimes with a gland (faint to showy) near apex, inner surface often glabrous; petals 5, often contorted in buds, variously coloured, smooth on both sides or sometimes rough and papillose inside; disc annular or 5 glands, fleshy to membranous, sometimes revoluted at apex; stamens 3 or 5, filaments united into an erect androphore, latter sometimes 3- or 5-cleft at top, anthers ellipsoid, either on free part of filaments or sessile at top of androphore, dorsifixed, 2-thecate, opening extrorse via longitudinal slits, sometimes divaricate at apex, connectives sometimes with numerous dark reddish droplets (or expanded cells) with secretion; pistillode absent. Pistillate flowers of same size or larger than staminate flowers; pedicel often thickened towards apex and accrescent in fruit; perianth as staminate flowers when flowering but sepals sometimes accrescent and petals early caducous; disc often same as staminate flowers, annular or 5 glands, often thin membranous; ovary globose, narrowed evenly towards apex into a style, 3-locular, each locule with a single ovule, outer wall glabrous to hairy; style short, often indiscernible; stigmas 3, linear, often thickened at base and bifid at top. Fruits capsules, subglobose, dehiscing septicidally and partly apically loculicidally into 3 bifid cocci; pedicel often elongating and thickened; sepals and stigmas often persistent; wall woody, exocarp often (partly) splitting off; columella persistent, T-shaped. Seeds depressed globose, smooth and marbled, ecarunculate.

Distribution — Circa 60 species, ranging from India to China, throughout SE Asia mainland and Malesia to NE Australia and the W Pacific; 38 species in Malesia.

KEY TO THE SPECIES

1.	Petiole short, shorter than 1.5 cm and shorter than 1/9 the length of the blade (in mature leaves) 2
1.	Petiole relatively long, longer than 1.5 cm or longer than 1/9 the length of the blade (in mature leaves)12
	Stem not branched (plant monocaul)
3.	Inflorescences longer than 7 cm; flowers never cauliflorous. — Sabah: Sandakan, Kabili-Sepilok FR
3.	Inflorescences shorter than 7 cm; flowers partly cauliflorous. — Malay Peninsula and Brunei 4

³ Throughout this part, an asterisk (*) refers to a specimen seen only as on-line image.

4.	Flowers reddish purple; stamens 3. — Brunei: Temburong	21.	Leaves larger than 16 by 6 cm. — Sarawak
4.	Flowers yellow; stamens 5. — Malay Peninsula: Lesong FR	21.	Leaves smaller than 16 by 6 cm. — Philippines
	Leaf blades densely hairy on upper side 11. <i>T. flavidus</i> Leaf blades glabrous on upper side (or slightly hairy when		Stamens 5. — Sumatra
6.	young)		Inflorescences not branched (no side-branches) 24 Inflorescences branched
6.	stems		Maximum petiole length less than 5.5 cm
7.	thyrses	25.	Pistillate flowers single per inflorescence; pistillate sepals accrescent
7.	ing subtended by big leaf-like bracts. — Malay Peninsula, Sumatra, Java, Bali 2. <i>T. aurantiacus</i> Flowers purplish black; stamens 5; pistillate inflorescences		Pistillate flowers more than 1 per inflorescence; pistillate sepals not accrescent
	absent, bracts small. — Sumatra: Alas River area		Leaf blades linear to long-lanceolate. — Sabah, Philippines
8.	Inflorescences (staminate ones if unisexual) racemose thyrses (no side branches)	26.	Leaf blades elliptic. — Philippines: Victoria Mountains
8.	Inflorescences (staminate ones if unisexual) paniculate thyrses (branching)		More (often much more) than 4 pistillate flowers present on inflorescences
9.	Young branches with reddish annular stripes. — Java	27.	Fewer than 4 pistillate flowers present on inflorescences 31b. <i>T. villosus</i> var. <i>borneensis</i>
9.	Young branches without reddish annular stripes. — Malay Peninsula, Sumatra, Java, Borneo, Philippines 10		Stamens 3 29 Stamens 5 31
	Stamens 5; fruits not warty. — Sumatra 4. <i>T. beccarii</i> Stamens 3; fruits warty. — Malay Peninsula, Sumatra, Java, Borneo, Philippines		Inflorescences mainly unisexual. — Malay Peninsula, Sumatra
11.	Petals elliptic or spathulate; stamens 5, anthers divari-	30.	Ovary glabrous 26. <i>T. scopulatus</i>
11.	cate		Ovary hairy
	Leaf blades hairy on upper side when mature 13 Leaf blades glabrous on upper side when mature 17	31.	Gunung Angsi
	Stamens 3 14 Stamens 5 16		Inflorescences branched not more than once
14.	Pistillate sepals greatly accrescent in fruits. — Malay Peninsula		Stamens 3 34 Stamens 5 35
14.	Pistillate sepals not much accrescent. — Sabah, Philippines		Petals entire, dark yellow. — New Guinea
	Staminate inflorescences paintbrush-like glomerules along rachis. — Philippines	34.	Petals bilobed, yellow or reddish. — Malay Peninsula, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands
	per node along rachis). — Sabah	35.	Pistillate sepals accrescent. — Malay Peninsula
16.	Plant with stellately bundled hairs all over (except on the upper surfaces of leaves, bracts and sepals). — Malay	35.	Pistillate sepals not accrescent. — New Guinea
	Peninsula: Endau Rompin and Gunung Panti		Main rachis of inflorescences shorter than 10 cm 37 Main rachis of inflorescences longer than 10 cm 38
	Plants with only simple hairs. — Malay Peninsula: Mawai – Jemaluang Road	37.	Stamens 5. — Malay Peninsula 6. <i>T. capillipes</i> Stamens 3. — Philippines 23. <i>T. polyanthus</i>
	Staminate flowers in glomerules	38.	Leaves triplinerved
	in racemose or paniculate thyrses (not glomerulate) 23 Each glomerule with at most 1 bract 19		Inflorescences often with very few flowers at one time. —
19.	Glomerules subtended by 2 or more bracts 22 Stamens 3 20 Stamens 5 21	39.	Sarawak
	Petioles up to 3.5 cm long. Inflorescences without leaf-like	40.	Branchlets and lower side of leaf blades densely hairy. —
20.	bracts. — Philippines	40.	Sumatra: Sikunder FR
	31d. <i>T. villosus</i> var. <i>merrillianus</i>		22. T. philippinensis

REGIONAL KEYS			Stamens 3				
Key to the species of the Malay Peninsula			Flowers orange				
1. F	Petioles shorter than 3.5 cm long and shorter than 1/10		Flowers purplish black				
1. F	ength of blade	7.	Inflorescences thyrsoid, auxillary or terminal; pistillate flowers at the end of rachis, pedicel c. 6 mm long, sepals very lightly pubescent				
2. F	Plants not branching; adventitious roots present. — Lesong FR	7.	Inflorescences absent; pistillate flowers solitary and cauliflorous, pedicel c. 1 mm long, sepals densely hirsutulous to sericeous				
3. L	Leaves densely hairy above		Inflorescences panicles, much branched 9 Inflorescences (raceme-like) thyrses or single glomerules, not branched				
4. \	Venation triplinerved (basal veins distinct from others), ateral veins often fewer than 9 pairs		Leaf blade densely pubescent, flowering branches tomentose				
5. L 6. I	Leaves and petiole totally glabrous 13. <i>T. laevigatus</i> Leaves slightly hairy beneath, petiole hairy		Inflorescences glomerules, subtended by two large leaf-like bracts 9. <i>T. dipteranthus</i> Inflorescences raceme-like thyses, without leaf-like bracts 18. <i>T. malaccanus</i>				
	nflorescences branched, less than 8 cm long	Ko	y to the species of Java				
7. 8	Staminate flowers cauliflorous; stamens 3		Venation triplinerved (basal veins distinct from others),				
7. 8	Staminate flowers in axillary thyrses; stamens 5		lateral veins often fewer than 9 pairs				
8. L 9. F	Leaf blades hairy		Leaves and petiole totally glabrous 13. <i>T. laevigatus</i> Leaves slightly hairy beneath, petiole hairy				
	ower layer soft	3.	Young branches without reddish annular stripes; staminate flowers cauliflorous 2. <i>T. aurantiacus</i>				
10. L	Lower layer hairs on petiole and midrib stellately bundled	3.	Young branches with reddish annular stripes; staminate flowers in racemes				
	nflorescences less than 3 cm long, stamens 5	Ke	y to the species of Borneo				
11. I 3	nflorescences (often far) more than 3 cm long, stamens 3		Venation triplinerved (basal veins distinct from others), lateral veins often fewer than 9 pairs				
12. I	around branches (cauliflorous) 26. <i>T. scopulatus</i> nflorescences of only one form, never grouped, never cau-		Inflorescences shorter than 4 cm long . 13. <i>T. laevigatus</i> Inflorescences longer than 4 cm long . 32. <i>T. viridissimus</i>				
13. I	iflorous		Petiole shorter than 2.5 cm or shorter than 1/10 length of leaf blade				
	nflorescences racemes; stamens 5. — Gunung Angsi.	Э.	leaf blade				
	nflorescences raceme-like thyses; stamens 3	4.	Flowers partly cauliflorous, inflorescences shorter than 7 cm				
		4.	Flowers never cauliflorous, inflorescences longer than 7 cm				
Key	to the species of Sumatra	_	7				
	Petioles less than 3.5 cm long		Plants not branched, adventitious roots present. — Brunei: Temburong				
	Venation triplinerved (basal veins distinct from others),	6.	Leaves glabrous above. — Sumatra, Sabah, Philippines				
2. \	ateral veins often fewer than 9 pairs	6.	Leaves pubescent above. — Sabah				
3. L	Leaves and petiole totally glabrous 13. <i>T. laevigatus</i> Leaves slightly hairy beneath, petiole hairy		Plants branched; petals (both sexes) 2–2.5 cm long				
4. I	nflorescences (often far) more than 7 cm long						
	nflorescences less than 7 cm long		Staminate flowers clustered into glomerules 9 Staminate flowers in racemes, panicles or thyrses 11				

9. Stamens 5. — Sarawak. 5. T. calcicolus 9. Stamens 3. 10			
10. Both staminate and pistillate flowers in a single glomerule on the top of peduncle			
10. Staminate flowers in several glomerules along the main rachis, pistillate inflorescences racemes			
31d. <i>T. villosus</i> var. <i>merrillianus</i>			
11. Inflorescences large panicles 8. <i>T. diffusus</i> 11. Inflorescences racemes or thyrses			
12. Leaf blade less than 1.5 cm wide			
Key to the species of the Philippines			
1. Petioles shorter than 3.5 cm 2 1. Petioles longer than 3.5 cm 10			

Kej	to the species of the Philippines
	Petioles shorter than 3.5 cm
2.	Venation triplinerved (basal veins distinct from others), lateral veins often fewer than 9 pairs
2.	Venation penninerved (basal veins identical to others), lateral veins often more than 9 pairs
	Leaves and petiole totally glabrous 13. <i>T. laevigatus</i> Leaves slightly hairy beneath, petiole hairy
	Leaves densely pubescent above 19. <i>T. merrillii</i> Leaves densely glabrous or glabrescent when young above
5.	Leaf blades: length more than 12 times width
5.	Leaf blades: length (often far) less than 12 times width 6
	Inflorescences (often far) more than 7 cm long
	Inflorescences less than 7 cm long
7.	Staminate inflorescences paniculate or paintbrush-like thyrses (with at least secondary branches)
7.	Staminate inflorescences racemes or raceme-like thyrses
8.	Leaves paler above (when dry); staminate inflorescences glomerules
8.	Leaves paler beneath (when dry); staminate inflorescences paintbrush-like thyrses 23. <i>T. polyanthus</i>
9.	Pistillate sepals much accrescent when fruiting
9.	Pistillate sepals not accrescent when fruiting
	Inflorescences large panicles 22. <i>T. philippinensis</i> Inflorescences short cymes clustered on a rachis 11

11.	Staminate flowers never cauliflorous; stamens 5
	15. <i>T. longipes</i>
11.	Staminate flowers often partly cauliflorous; stamens
	31d. T. villosus var. merrillianus

Key to the species of The Lesser Sunda Islands

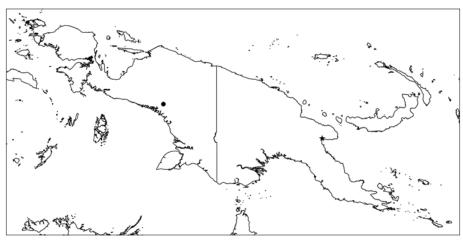
Key to the species of New Guinea

1.	Stamens 3	1.	Т. ар	etalogyne
1.	Stamens 5		12.	T. hartleyi

1. Trigonostemon apetalogyne Airy Shaw — Map 1

Trigonostemon apetalogyne Airy Shaw (1979) 534; (1980b) 206. — Type: Kostermans & Soegeng 340 (holo K; iso BO, L), [Indonesia,] W Papua, limestone hills E of Sukarnapura (= Hollandia = Djajapura), Polima I.

Small trees, at least 2.5 m tall, stem at least 4 cm diam; flowering branches c. 3 mm diam. Outer bark c. 0.15 mm thick. smooth, dark brown to grey, appressed pubescent on young parts; inner bark c. 2 mm thick, blackish; wood reddish brown. Stipules subulate to falcate, 0.8-1 mm long, base pubescent, apex slightly bent. Leaves: petiole terete but grooved above. 2.5-5 cm long, slightly pubescent to glabrescent, slightly thickened at both base and top; blade oblanceolate, 11-20 by 3.5-7 cm, chartaceous to coriaceous, base narrow-rounded, with 2 adaxial glands, margin distantly serrate, apex acuminate, both sides glabrous (very sparsely pubescent when young); venation penninerved, slightly pubescent on lower side when young, midrib flat above and elevated beneath, secondary nerves 9-12 pairs, small veins reticulate, often obscure. Inflorescences: unisexual; staminate flowers cauliflorous; pistillate inflorescences subterminal, up to 14 cm long, paniculate (one side branch), few-flowered at the apex of the branches; bracts lanceolate, 0.8-2 by 0.4-0.9 mm, apex acuminate, pubescent outside. Staminate flowers c. 5 mm diam; pedicel 3-5 mm long, glabrescent; sepals ovate to orbicular, 1–1.2 by 0.6–0.7 mm, glabrescent outside; petals elliptic to obovate, 2-2.5 by 1.2-1.8 mm, entire, dark yellow, glabrous; disc glandular; stamens 3, androphore 0.3-0.5 mm long, filaments 0.1-0.2 mm long, anthers ellipsoid, c. 0.2 mm long. Pistillate flowers withered (post-anthesis), c. 2.5 mm diam; pedicel c. 7 mm long and 0.8 mm diam (top) when flowering, slightly thickened towards apex, in fruit accrescent to c. 1.5 cm long and 1.3 mm diam (top),



Map 1 Distribution of *Trigonostemon apetalogyne* Airy Shaw (♠); *T. hartleyi* Airy Shaw (★).



Fig. 1 Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl., cultivated in Bogor Botanical Garden (XV.J.A.XXXI.15, originally from Indo-China), Java, Indonesia. a. Growing habit; b. leaves; c. short branch with cauliflorous flowers; d. staminate flowers; e. fruit. — Photos by Ren-Yong Yu.

glabrescent; sepals elliptic, 1.5–2 by 0.5–1 mm, glabrescent; petals not seen; disc as staminate flowers; ovary c. 1 mm diam, glabrous; style indiscernible; stigmas c. 0.6 mm long, apically flattened and slightly bifid. *Fruits* and *seeds* unknown.

Distribution — New Guinea (endemic).

Habitat & Ecology — On limestone hills. Altitude: c. 100 m. Flowering and fruiting: August.

Notes — 1. The species is only known from the type collection. The specific epithet indicates that the pistillate flowers lack petals, but this is very unlikely, because the petals are generally early cauducous in *Trigonostemon* and the specimen only has old flowers.

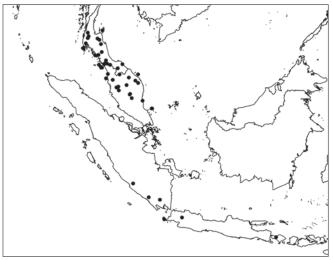
- 2. *Trigonostemon apetalogyne* differs from *T. hartleyi* only by having 3 instead of 5 stamens.
- 3. This species is also similar to *T. villosus* var. *borneensis* in leaf shape and cauliflorous staminate flowers, but we still keep it separate because of its dark yellow flowers (as recorded on the type collection; vs dark purplish in *T. villosus* var. *borneensis*) and branched pistillate inflorescences (vs not branched in *T. villosus* var. *borneensis*).

Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl. Fig. 1; 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; (1972a) 345, f. 11; Whitmore (1973) 136; Airy Shaw (1974) t. 3721; (1981) 352; Chantar. (2007) 576. — Tylosepalum aurantiacum Kurz ex Teijsm. & Binn. (1864) 50. — Codiaeum aurantiacum (Kurz ex Teijsm. & Binn.) Müll.Arg. (1866) 1118. — Lectotype (designated here): Teijsmann s.n. (L, barcode L.2260196), Indonesia, Java, cultivated in Bogor Botanical Garden (originally from Bangka?).

Actephila aurantiaca Ridl. (1923) 360; (1924) 197. — Type: Ridley s.n., Feb. 1917 (holo K, barcode K000959323), Malaya, Kelantan, Chaning Woods. Actephilopsis malayana Ridl. (1923) 361; (1924) 252; M.R.Hend. (1939) 68. — Trigonostemon malayanus (Ridl.) Airy Shaw (1967) 413. — Syntypes: Curtis 674 (K), Malaya, Penang, Ayer Hitam; Haniff 1611 (?), Malaya, Perak, Gunung Kerbau; Ridley 2300 (K), Malaya, Pahang, Kwala Tembeling.

Shrubs or small trees, 1.5–3(–6) m tall, stem up to 10 cm diam; flowering branches up to 2 mm thick, smooth, brownish. *Bark* c. 2 mm diam; sap red and sticky; wood pale brown. *Stipules* subulate, c. 1.5 mm long, hirsute. *Leaves*: petiole 0.5–3 cm long (depending on leaf size), slightly wrinkled and grooved above, more or less pubescent; blade elliptic to oblong, 8–30



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

by 2.5-12 cm, chartaceous to coriaceous, base acute, with 2 glands adaxially, occasionally developing into stipellae, margin distantly serrate, teeth falcate or subulate, apex acuminate, young blade reddish, mature ones dark green above, light green beneath, glabrous or scattered pubescent on lower side; venation penninerved, midrib slightly raised above, distinctly elevated beneath, nerves 8-13 pairs, straight, branched and connected near margin, small veins reticulate, often obscure. Inflorescences: staminate ones cauline, few short and condensed thyrses, often bracteolate and with 1 flower per node; pistillate ones terminal or axillary, often racemose or paniculate, sometimes mixed with a few staminate flowers; bracteate under each branch and flower, the main rachis (and sometime secondary rachises) often subtended by large, leaf-like bracts, shortly (up to 5 mm) petiolate, blade elliptic or ovate, up to 7 by 3.5 cm, base often cordate, apex acuminate. Staminate flowers c. 6 mm diam; pedicel very slender, up to 1 cm long, c. 0.1 mm diam, pinkish, glabrous; sepals unequal, oblong, 1.2-1.5 by 0.5–1 mm, imbricate, yellowish or reddish, connate at base, apex rounded, more or less pubescent outside, with an often showy gland in the middle outside; petals oblong, c. 4 by 1.3 mm, orange, with a reddish honey mark at base, visible on both sides, inside often paler and outside sometimes with whitish margin, few parallel veins often visible, apex acute, glabrous on both sides; disc glands more or less trapezoid, thick and fleshy, c. 0.2 by 0.5 mm, c. 0.2 mm thick, apex flat; stamens 3, androphore erect, c. 0.5 mm long, trifid at top, anthers free, divaricate, each theca c. 0.6 by 0.2 mm. Pistillate flowers c. 5.5 mm diam, pedicel thickening towards apex, up to c. 7 mm long, apically c. 0.7 mm diam when flowering, up to c. 2 cm long and apically c. 1 mm diam when fruiting, glabrous; sepals as in staminate flowers, persistent in fruits; petals obovate, c. 3.5 by 2 mm, orange outside and paler inside, base cuneate or somewhat claw-like, with a reddish (dark reddish pigment granules in epidermis cells visible) honey mark, apex often rounded; disc lobes broad, almost rectangular, truncate at apex, c. 0.3 by 0.7 mm, thin, membranous; ovary c. 1.1 mm diam, glabrous, light yellowish; styles short, c. 0.2 mm long, stigmas 3, light yellowish, slightly thickened, apically split and somewhat horseshoe-shaped. Fruits c. 1.2 cm diam, greenish to reddish, glabrous; sepals not accrescent; wall c. 1 mm thick; columella c. 5.5 mm long. Seeds c. 5.5 mm diam, dark orange when dry, hilum somewhat heart-shaped or rhombic, c. 1.5 mm diam.

Distribution — Thailand, Malay Peninsula, Sumatra, Java, Bali

Habitat & Ecology — Lowland evergreen (often dipterocarp) forests, growing in understorey on limestone, along streams or on hill slopes. Altitude: 0–600 m. Flowering and fruiting: all year round.

Notes — 1. A species variable in shape and size of the leaves. It shows similarities with *T. wildeorum*, from which it can easily be differentiated by its racemose or paniculate pistillate inflorescences (vs pistillate flowers always inserted in leaf axils and the pistillate sepals always strongly accrescent in *T. wildeorum*).

2. One specimen (*P.E. Schmutz 524*, Lesser Sunda Islands, Flores) with elliptic and dark brownish to greyish leaves and a short (c. 1.5 cm) staminate peduncle, seems to be an intermediate form between *T. aurantiacus* and *T. hartleyi* (endemic to New Guinea), and even the location of the collection is between W Malesia and New Guinea. Since no other specimens are known and *T. hartleyi* is a poorly understood species, this specimen cannot be accurately identified and the Lesser Sunda Islands is here not included in the distribution of *T. aurantiacus*.

Trigonostemon balgooyi R.Y.Yu & Welzen, sp. nov. — Fig. 2; Map 3

This species strongly resembles *T. merrillii* and *T. villosus*, but differs by its appressed stellately bundled hairs, cordate bracts subtending the pistillate flowers and staminate flowers with 5 instead of 3 stamens. — Type: *M.M.J. van Balgooy 7102* (holo L; iso K, KEP, SAN), Malaysia, Johor, Endau-Rompin, Kuala Jasin, N2°32' E103°22'. Paratypes: *Sinclair 10598* (K, SING; E, NY not seen), Malaysia, Johor, Gunung Panti, Waterfall, Lombong; *KEP FRI (Kamarul Hisham et al.) 73820* (K, KEP, SAN, SING; BKF not seen), Malaysia, Johor, Endau-Rompin S.P., Bagoh camp area; *KEP FRI (Kamarul Hisham et al.) 73826* (KEP), Malaysia, Johor, Mersing, Endau-Rompin S.P., trail to Kuala Kembah camp from Bagoh; *Stone 8719* (KLU), Malaysia, Johor, Kota Tinggi, Ayer Terjun.

Shrubs or small trees, 2–3 m tall, dbh 1.5–3 cm; flowering branches 3–4 mm diam. *Indumentum* consisting of 2 layers of

hairs (except on sepals and upper surface of leaves and bracts, these glabrous or with only 1 layer of hairs), upper layer hispid, with simple long and rigid golden hairs, lower layer of stellately bundled hairs consisting of 3–5 tiny, appressed, whitish hairs originating from one papillose point. *Outer bark* c. 0.1 mm thick, dark brownish to greyish, hairy, often slightly fissured; inner bark 0.1–0.2 mm thick, whitish to reddish to brownish, often with sap (solidified when dry); wood creamy, reddish brown. *Stipules* subulate, c. 0.5 mm long, caducous. *Leaves*: petiole terete, 1.5–6 cm long, 1–1.5 mm diam, hairy; blade oblong to oblanceolate, 12–23 by 1.5–6 cm, chartaceous, base cuneate to acute, with 2 nipple-like glands adaxially, margin distantly serrate, teeth small, falcate, apex acuminate to caudate, upper surface medium green, slightly bullate, papillose hispid (no stellate hairs), lower surface pale green, papillose hispid and

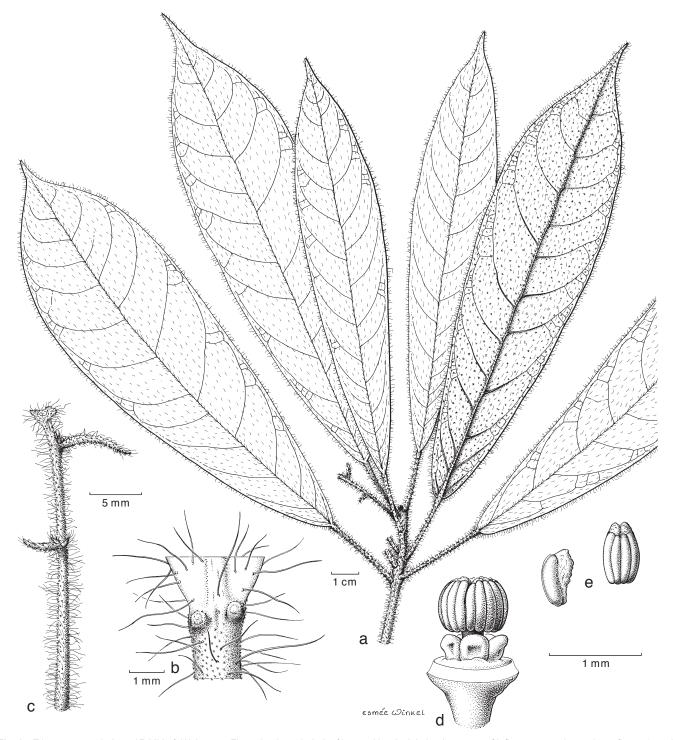


Fig. 2 Trigonostemon balgooyi R.Y.Yu & Welzen. a. Flowering branch; b. leaf base with adaxial glands; c. part of inflorescence; d. staminate flower (sepals and petal removed); e. anthers, front and lateral views (all: Van Balgooy 7102, L). — Drawing by Esmée Winkel, 2016.

with stellately bundled hairs on venation; venation penninerved, midrib slightly elevated above and distinctly elevated beneath, nerves 9-11 pairs, curved and bow-shaped, narrowed and connected along margin, veins reticulate, often obscure above. Inflorescences: staminate ones pyramidal paniculate or racemose, sometime cauliflorous, rachis at least up to 9 cm long, c. 1 mm diam (lower part), hispid and with stellately bundled hairs; bracts lanceolate, up to 7.5 by 1.3 mm, sparsely papillose hispid above, hispid and with stellately bundled hairs beneath; pistillate ones often single-flowered, peduncles 4-6 cm long, c. 0.6 mm diam (evenly wide throughout), sparsely hispid; bracts in lower part often 1.3-1.8 by 0.4-0.5 cm, hispid and with sparse stellately bundled hairs; bracts subtending the pistillate flower cordate, 1.5–2.1 by 0.6–1.2 cm, palmately veined, sparsely hispid above and hispid and with sparse stellately bundled hairs (often along veins) beneath. Staminate flowers c. 7 mm diam; pedicel indiscernible; sepals elliptic, 1-1.5 by c. 1 mm, pale green, sparsely papillose hispid outside, glabrous inside; petals elliptic, c. 3.3 by 2.5 mm, red to maroon, both sides glabrous, sometimes with a few pustules; disc lobes glandular, 0.25-0.3 by 0.3-0.6 mm, deep purple, apex rounded, slightly recurved; stamens 5, androphore c. 0.7 mm long, 5-cleft at apex; anthers ellipsoid, each theca 0.5-0.6 mm long, connectives apically with dark purplish droplets (or expanded cells) with secretion. Pistillate flowers c. 1.2 mm diam; pedicel less than 5 mm long; sepals triangular, c. 6.5 by 4.5 mm, apex acuminate, hispid outside, sparsely hispid and with sparse stellately bundled hairs (often along veins) inside; petals orbicular, 6-7 by 5-6.8 mm, maroon; disc not seen; ovary c. 1.2 mm diam, sparsely hairy; style c. 0.2 mm long, stigmas deeply divided, free parts c. 1.5 mm long. Fruits: sepals (remnants) persistent, 1.3-1.5 by 0.55-1 mm, with sparse stellately bundled hairs outside, glabrous inside; columella 5.5-7 mm long; cocci white, with a few hairs when young and nearly glabrous when mature; wall c. 0.65 mm thick, exocarp not detaching. Seeds c. 6 mm diam, brown when dry.

Distribution — Malay Peninsula (endemic).

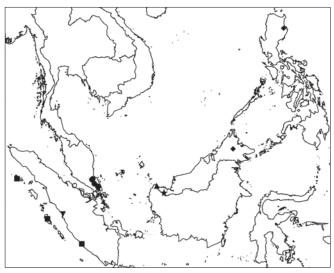
Habitat & Ecology — Lowland primary (dipterocarp) rainforest on clay soil on hillside or riverside. Flowering: March to April, July; fruiting: July.

Note — The only species in Malesia that has stellately bundled hairs, which makes it quite unique (*T. reidioides* in Thailand and Indochina also has stellately bundled hairs). The cordate bracts of the pistillate flowers are also distinct. The pistillate disc was not seen because it was covered by petals in the only flower present on the available material.

4. *Trigonostemon beccarii* Ridl. — Fig. 3; Map 3

Trigonostemon beccarii Ridl. (1925) 89; Jabl. (1963) 165; Airy Shaw (1981) 353. — Type: Beccari PS 965 (K, L), Sumatra, Padang, Sungei Buluh. Trigonostemon longisepalus Ridl. (1925) 89; Jabl. (1963) 165. — Type: Brooks 8274 (holo K), Sumatra, Lubok Tandai.

Shrubs; flowering branches 1.6–4.5 mm diam, sometimes hollow. *Outer bark* 0.1–0.2 mm thick, brownish to greyish, smooth; inner bark 0.1–0.2 mm thick, dark reddish brown; wood white to pale reddish brown. *Stipules* falcate, 0.5–0.7 mm long, glabrous. *Leaves*: petiole 0.25–1.5 cm long, grooved above, glabrous to glabrescent; blade oblong to oblanceolate, 8–28 by 1.5–7 cm, base cuneate, adaxially 2 glands present but caducous, margin slightly distantly serrate, apex acuminate, upper side dark greenish, lower side pale green, both sides glabrous; midrib slightly raised on both sides, nerves 10–14 pairs, very slightly raised beneath, often obscure, small nerves reticulate, obscure. *Inflorescences* bisexual, axillary to subterminal, often 1 pistillate flower on the top and few short scorpioid cymes (glomerules) of staminate flowers along the



Map 3 Distribution of *Trigonostemon balgooyi* R.Y.Yu & Welzen (♠); *T. beccarii* Ridl. (■); *T. calcicolus* (R.I.Milne) R.Y.Yu & Welzen (★); *T. diffusus* Merr. (♠); *T. dipteranthus* Airy Shaw (▼); *T. filiformis* Quisumb. (♠).

rachis below; rachis 3–12 cm long, 0.5–0.7 mm diam, glabrous; bracts elliptic to lanceolate, 0.7–1.5 by 0.3–0.6 mm, glabrous to pubescent, apex acuminate to rounded. Staminate flowers c. 4.5 mm diam; pedicel c. 3.5 mm long, c. 0.3 mm diam, glabrescent; sepals elliptic, c. 1 by 0.7 mm, apex rounded, slightly ciliate on margin, glabrescent outside; petals elliptic, 1.5-2.2 by 1.2–1.5 mm, margin entire, apex rounded, glabrous outside, rough and papillose inside; disc lobes semi-orbicular to nearly lanceolate, c. 0.5 by 0.5 mm, apex rounded, glabrous; stamens 5, androphore c. 0.5 mm long, 5-cleft at the top, anthers ovoid to ellipsoid, c. 0.6 mm long, free, thecae slightly divaricate at apex, connectives apically with numerous droplets (expanded cells) with secretion. *Pistillate flowers* 2.5–3.5 mm diam; pedicel slightly thickened towards apex, c. 6 mm long, apically 0.7-1 mm diam when flowering, accrescent to 2.5 cm long and apically 2 mm diam when fruiting, glabrous to glabrescent; sepals ovate, 1.4-1.7 by 1-1.5 mm, apex acute, slightly pubescent to glabrescent outside; petals (remnants) nearly elliptic, c. 2.1 by 0.8 mm, glabrous outside, rough and scurfy inside; disc lobes as staminate flowers; ovary 1–1.5 mm diam, densely pubescent; styles indiscernible; stigmas completely bifid, each arm c. 1 mm long, thickened at base, slender and often bent upward. Fruits c. 1 cm diam, appressed pubescent; sepals persistent but not accrescent; wall c. 0.5 mm thick, exocarp partly detaching; columella c. 6.5 mm long. Seeds 4.2–5.5 mm diam, pale brown when dry, hilum heart-shaped or rhombic, c. 1.2 by 1–1.2 mm.

Distribution — Sumatra (endemic).

Habitat & Ecology — Flowering and fruiting: September.

Note — A distinct species with short petiole, inflorescences of short glomerules along an erect rachis and 5 stamens in the staminate flowers. Ridley (1925) described *T. beccari* and *T. longisepalus* as separate species but he did admit that these two species were possibly based on two sexes of one plant. Our recent collection *R. Y. Yu 169* (L), from the Bogor Botanical Gardens (XI.B.XVII.270-270a, originally from Sumatra), bears both the same staminate and pistillate structures as described in Ridley (1925), and thereby confirms the conspecific status of *T. beccari* and *T. longisepalus*.

Trigonostemon calcicolus (R.I.Milne) R.Y.Yu & Welzen, comb. nov. & stat. nov. — Map 3

Trigonostemon polyanthus Merr. var. calcicolus R.I.Milne (1995a) 28, in key, 30, in key, 33, f. 1. — Type: Chew Wee-Lek 679 (holo K; iso L), Sarawak, 1st Division, Kuching District, Tiang Bekap, Mt Mentawa, N1°12' E110°23'.



Fig. 3 Trigonostemon beccarii Ridl., cultivated in Bogor Botanical Garden (XI.B.XVII.270, originally from Sumatra), Java, Indonesia. a. Growing habit; b. leaves; c. inflorescence with staminate flowers; d, e. fruit. — Photos by Ren-Yong Yu.

Small trees, 3 m tall; flowering branches c. 3 mm diam. Outer bark c. 0.1 mm thick, brownish, pubescent to hirsutellous when young, hairs short and stiff; inner bark c. 0.1 mm thick, dark reddish; wood pale brown to reddish brown. Stipules subulate, c. 0.7 mm long, caducous, hirsutellous. Leaves: petiole 4.6-9 cm long, terete but grooved above, hirsutellous; blade broadly elliptic, 16-23.5 by 7-11.5 cm, base acute to rounded, adaxially 2 glands present but caducous, margin entire or slightly distantly serrate, ciliate, apex acuminate to rounded, upper side dark brown to black (when dry), glabrous, lower side brown (when dry), scarcely pubescent to hirsutellous; midrib slightly raised and glabrous above, distinctly elevated and hirsutellous beneath, nerves 9-13 pairs, slightly raised and hirsutellous beneath, small nerves reticulate, obscure. Inflorescences axillary, unisexual; staminate ones thyrsoid, flowers clustered into few very short cymes (nearly a glomerule) at apex of rachis, rachis 2.5-5 cm long, 0.6-0.9 mm diam, hirsutellous; bracts to glomerules elliptic to lanceolate, 7–15 by 1.5–5 mm, apex acute to acuminate, hirsutellous outside, bracts to the flowers small, triangular to lanceolate, c. 0.3 by 0.1 mm, hirsutellous outside; pistillate inflorescences similar to staminate ones but with fewer

flowers, 7-10 cm long, 0.7-1.1 mm diam, hirsutellous; bracts to the flowers lanceolate, c. 5 by 1.5 mm, hirsutellous outside. Staminate flowers (unopened) 1.1–1.6 mm diam; pedicel 0.5–2 mm long, 0.3-0.5 mm diam (apex), thickened towards apex, densely hirsutellous; sepals elliptic, 0.5-1 by 0.3-0.5 mm, apex acute to rounded, hirsutellous outside; petals orbicular to elliptic, 0.5-0.6 mm diam, black, glabrous on both sides; disc indiscernible; stamens 5, androphore indiscernible, anthers ellipsoid, c. 0.4 mm long, connectives with apically some droplets (expanded cells) with secretion. Pistillate flowers: sepals triangular, c. 3 by 1 mm, green, thin, pubescent outside; petals elliptic-ovate, c. 1.2 by 1 mm, black, glabrous; disc insignificant; ovary strongly pyriform, c. 0.8 mm diam, glabrous, yellow; stigma slightly divided. Fruits (Milne 1995a): oblong-ovate, c. 9 by 8 mm; pedicel c. 10 mm long, pubescent; sepals persistent, puberulous, drying brownish grey. Seeds unknown.

Distribution — Borneo (Sarawak, endemic).

Habitat & Ecology — On limestone. Altitude: recorded once from 80 m. Flowering: July.

Note — The descriptions of the pistillate flowers and fruits are based on Milne (1995a). This species is only known from

the type collection from Sarawak. The species has the same characteristics of *T. villosus* var. *merrillianus* (e.g., long petiole, glomerules on inflorescences), but has 5 instead of 3 stamens. Since the number of stamens is generally reliably constant per species, this taxon is here regarded as a distinct species rather than a variety as it is in Milne (1995a).

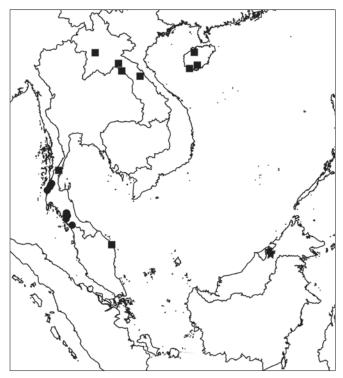
6. Trigonostemon capillipes (Hook.f.) Airy Shaw — Map 4

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

Trigonostemon pachyphyllus Airy Shaw (1971) 546; Chantar. (2005) 27; (2007) 581. — Type: Kerr 19429 (holo K), Thailand, Chanthaburi, Khao Soi Dao

Trigonostemon sp. nov., aff. indicus (Baill.) Müll.Arg.: Jabl. (1963) 168. — Voucher: Kiah 35303 (BO, K, L, SING), Malaysia, Perlis, Bukit Kaki.

Shrubs or small trees, 1–8 m tall; flowering branches 1.7–3.2 mm diam. Bark 0.1-0.2 mm thick, brownish to greyish, slightly pubescent near young parts, smooth; wood pale yellowish. Stipules subulate, 0.5-1 mm long, caducous, pubescent at base. Leaves: petiole 0.3-1(-2.5) cm long, grooved above, pubescent; blade oblanceolate, oblong or obovate, 9-20 by 3-7 cm, chartaceous, base acute to obtuse, with 2 adaxial glands, margin distantly serrate, teeth small, falcate, apex acuminate, upper side glabrous, lower side paler, slightly pubescent and more or less ciliate along margin; midrib slightly raised on both sides, nerves 9-12 pairs, connected along margin, small veins reticulate. Inflorescences: staminate ones thyrsoid, branched (paniculate), 4-8 cm long, glabrescent, axillary or cauliflorous; bracts leaf-like, elliptic to oblong, up to 10 by 4 mm, slightly pubescent abaxially; pistillate inflorescences cymose, peduncles slender, 1–15 cm long, 0.2–0.5 mm diam, often only one flower at top (sometimes with few depauperate flowers below); bracts as in staminate inflorescences, 4-20 by 1-5 mm. Staminate flowers c. 6 mm diam; pedicel 0.2-0.4 cm long, 0.1 (middle part)-0.2 (top) mm thick, glabrescent or



Map 4 Distribution of *Trigonostemon capillipes* (Hook.f.) Airy Shaw (●);
T. detritiferus R.I.Milne (★);
T. flavidus Gagnep. (■).

slightly pubescent; sepals elliptic, c. 1.6 by 1.2 mm, pale green, apex rounded or slightly notched, under the notch often with a gland on outside surface, but sometimes faint or only a few expanded cells; petals elliptic or spathulate, 3-3.5 by 1.5-1.8 mm, base narrowed, acute to cuneate, sometimes claw-like, entire, apex rounded, dark purple, in mature flowers with an orange flame-like honey mark in the middle of the lower part, smooth and glabrous outside, rough and papillose inside; disc lobes almost obtrapezoid, c. 0.35 by 0.3 mm, c. 0.1 mm thick, apex thickened and slightly reflexed, glabrous; stamens 5, androphore c. 0.6 mm long, c. 0.2 mm diam, 5-branched at c. 0.1 mm below apex, filaments c. 0.1 mm long, anthers c. 0.7 mm long, pinkish, divaricate, connectives apically with numerous dark reddish droplets (or expanded cells) with secretion. Pistillate flowers c. 1 cm diam, pedicel slightly thickening towards apex, 6-9 mm long, apically c. 0.7 mm diam when flowering, in fruit accrescent to 1.5 cm long and apically c. 2 mm diam, slightly pubescent; sepals oblong to lanceolate, c. 4 by 2 mm when flowering, accrescent to 5–15 by 2–6 mm in fruit, pale green, margin slightly serrate, teeth glandular, apex acute to acuminate; petals as staminate flowers but larger, c. 5 by 2 mm; disc lobes rectangular, c. 0.4 by 0.6, apex truncate, corners rounded; ovary c. 1 mm diam, densely hairy, style c. 0.1 mm long, often indistinct, stigmas nearly completely divided, c. 0.9-1 mm long, free arms c. 0.8 mm long, slightly thickened abaxially. Fruits c. 1.2 cm diam, finely hairy; sepals and stigmas persistent, stigmas flattened at base, abaxially hairy; wall c. 0.4 mm thick, exocarp not detaching; columella c. 5 mm. Seeds c. 6 mm diam; hilum heart-shaped, 1-1.6 by 1.4-1.5 mm.

Distribution — Thailand, Malay Peninsula,

Habitat & Ecology — Lowland rainforest to mangrove forest. Altitude: 0–300 m. Flowering: December to April; fruiting: December to February.

Note — Airy Shaw (1967) transferred this species from *Dimorphocalyx* to *Trigonostemon* without any information on staminate flowers in the type collection. Nevertheless, it can be recognized by the often single-flowered pistillate inflorescences and much enlarged sepals in pistillate flowers, and it differs from the newly proposed Philippine species *T. victoriae* by having thyrsoid staminate inflorescences and 5 instead of 3 stamens.

7. Trigonostemon detritiferus R.I.Milne — Fig. 4; Map 4

Trigonostemon detritiferus R.I.Milne (1994) 446, f. 2; (1995a) 27, in key, 28, in key. — Type: *Dransfield 6913* (holo K; iso BRUN), Brunei, Teburong District, Selapon.

Small trees, up to 2.5 m tall, 5–12 mm diam, without branches, adventitious roots present at the top of the main branch, 0.2–0.5 mm thick, much branched and curly, dirty and puberulent. Outer bark 0.3-0.4 mm thick, brownish; inner bark 0.5-0.6 mm thick, dark reddish, sap reddish; sapwood c. 1.6 mm thick, yellowish; heartwood c. 2.5 mm diam. Stipules subulate, c. 1.3 by 0.5 mm, pubescent, caducous. Leaves clustered on top of the stem; petiole 0.4-1 cm long, 2-2.5 mm diam, wrinkled and slightly pubescent, upper side flat, lower side rounded; blade oblanceolate, 20-45 by 5.5-10 cm, chartaceous, base rounded to cuneate, adaxial glands not seen, margin distantly serrate, teeth falcate, apex acuminate to almost caudate, upper side glabrous, lower side paler, densely pubescent on especially the venation; venation penninerved, midrib robust, slightly raised on both sides, nerves 15-30 pairs, curved, veins scalariform, veinlets reticulate. Inflorescences: staminate ones flowers single and cauliflorous, axillary, on upper part of branch, or thyrses inserted at leaf axils, 1-7 cm long, few-branched and few-flowered, rachis appressed puberulous; bracts linear to lanceolate, 2-20 by 0.3-6 mm, puberulent; pistillate ones

single, inserted at leaf axils. Staminate flowers: pedicel up to 4 mm long; sepals elliptic, 1–1.5 by 0.5–0.8 mm, pubescent outside, glabrous inside; petals obovate, 2–3 by 1–1.8 mm, apex rounded, reddish purple, glabrous; disc glandular, yellowish, c. 0.15 diam; stamens 3, androphore c. 0.5 mm long, anthers pinkish, ellipsoid, 0.4–0.5 mm long. Pistillate flowers: pedicel up to 3.5 cm long, puberulous; sepals and petals as in staminate flowers; disc glands glandular, c. 0.15 mm diam; ovary 0.25–1 mm diam, glabrous to pubescent; styles trifid, indistinct, stigmas slightly to deeply bifid. Fruits c. 6 mm diam, sometimes only one locule mature, other two aborted. Seeds opalescent when young, dark brownish when mature, marbled. Seedling: cotyledons 2, sessile, round, light green, triplinerved. First true leaf subsessile, obovate, base cordate, apex acute, blade light green.

Distribution — Borneo (Temburong District of Brunei, endemic).

Habitat & Ecology — Primary mixed dipterocarp forest, near rivers (c. 30–300 m away from river bank). Flowering and fruiting: June to November.

Notes — 1. The species strongly resembles *T. wetriifolius* in the growing habit, cauliflorous flowers and adventitious roots, while the distinct differences lie in the dark reddish (vs pale yellowish in *T. wetriifolius*) petals and 3 (vs 5 in *T. wetriifolius*) stamens.

2. This species has a special living strategy (also seen in *T. wetriifolius*, see Airy Shaw & Ng 1978). The leaves are always clustered on the top of the main branch, where the adventitious roots also generate, thus the leaves accumulate dirt and fallen leaves from inside and form humus, from which the nutrition can be absorbed by the adventitious roots.



Fig. 4 *Trigonostemon detritiferus* R.I.Milne, from Kuala Belalong, Temburong, Brunei. a. Growing habit; b, c. short branch, showing bark and cauliflorous flowers; d. top view of the tree, leaves arranged in whorls and used to trap fallen leaves; e. reddish exude; f. staminate flower; g. pistillate flower; h. fruit; i. seedling with 2 cotyledons; j. true leaves growing from the seedling. — Photos by: a–h: Ren-Yong Yu; i, j: Ferry Slik.



Fig. 4 (cont.)

8. Trigonostemon diffusus Merr. — Map 3

Trigonostemon diffusus Merr. (1928) 525; Jabl. (1963) 164; R.I.Milne (1995a) 27, in key, 29, in key, 46. — Type: *Mjöberg 145* (BM, K, UC*), Sarawak, Mount Poi

Shrubs or small trees, at least up to 6 m tall; flowering branches terete, 2-2.5 mm diam. Outer bark c. 0.1 mm thick, pale, slightly hirsute in young parts, glabrous and wrinkled in older parts; inner bark c. 0.2 mm thick, reddish brown; wood pale yellowish. Stipules falcate, 0.6-1 mm long, pubescent. Leaves: petiole 1-9 cm long, slightly pubescent, grooved above, thickened at base and top; blade oblong, 12-19 by 3.5-5.5 cm, membranous, sometimes slightly asymmetric, base acute and often with 2 adaxial glands, margin distantly crenate-dentate, teeth somewhat nipple-like, apex acuminate to caudate, surfaces olive-green, glabrous above and slightly hirsute beneath; midrib raised on both sides, slightly hirsute beneath, nerves 10-12 pairs, veins reticulate. Inflorescences paniculate, large and diffuse, much developed and branched but few flowers present, up to 35 cm long, slightly hirsute; bracts triangular, up to 0.6 by 0.3 mm, abaxial surface slightly pubescent. Staminate flowers (unopened) caducous, c. 1.7 mm diam; pedicel 2-3 mm long, 0.1-0.2 mm diam, glabrescent; sepals elliptic to ovate, 0.9-1.2 by 0.8-1 mm, slightly pubescent outside; petals elliptic, c. 1.5 by 1 mm, dark red or purple, margin slightly ciliate, apex rounded, both sides glabrous; disc lobes almost trapezoid, c. 0.2 by 0.3 mm; stamens 3, androphore c. 0.5 mm long, anthers ellipsoid, c. 0.6 mm long, connectives apically with numerous droplets with secretion. Pistillate flowers and fruits unknown.

Distribution — Borneo (Sarawak, endemic).

Habitat & Ecology — Forests near the foot of mountains. Altitude: 760 m. Flowering: September.

Notes — 1. The species is only known from two collections (the type and *J.W. Purseglove P. 4702*). It is mainly distinguished by its large, diffuse, few-flowered inflorescences.

2. *Trigonostemon diffusus* subsp. *condensus*, should be synonymised under *T. polyanthus*, see note 3 under *T. polyanthus*.

9. Trigonostemon dipteranthus Airy Shaw — Map 3

Trigonostemon dipteranthus Airy Shaw (1966) 47. — Type: Korthals s.n. ('853') (holo L), Sumatra, West Coast Res., Padang Region.

Small trees, 4.5–6 m tall; flowering branches terete or wrinkled, 3-3.5 mm diam, slightly pubescent when young, glabrescent when mature. Outer bark smooth, pale brownish; inner bark c. 0.2 mm thick; wood white. Stipules falcate or subulate, 0.5–1 mm long, often pubescent. Leaves: petiole terete but sometimes slightly grooved above, 3-12.5 cm long, middle part 1-1.5 mm diam, more or less pubescent, often slightly thickened at base and apex; blade oblong to elliptic or slightly oblanceolate, 15-22 by 4.5-8 cm, membranous, base acute or narrowed rounded, margin slightly distantly crenate-serrate, teeth often small, nipple-like or falcate, apex caudate, tip 1.5-2.5 cm long, upper side glabrous, lower side pubescent and paler; midrib flat and glabrescent above, elevated and pubescent beneath, nerves 10-12 pairs, curved and narrowed along margin, pubescent beneath, veins reticulate. Inflorescences axillary bisexual glomerules; peduncles slender, 2-6.5 cm long, finely appressed pubescent, flowers densely clustered at the top of peduncles and subtended by 2 conspicuous bracts; bracts opposite, almost sessile, widely ovate, 2-3.5 by 1.3-2.4 cm, membranous, base rounded or slightly emarginate, margin nearly entire, apex apiculate or acute, upper side glabrous, lower side appressed puberulent, especially along nerves. Staminate flowers c. 6 mm diam; pedicel c. 2 mm long, c. 0.3 mm diam, glabrescent; sepals elliptic, c. 1.2 by 0.6 mm, base connate, apex acute, sparsely puberulent outside; petals obovate, c. 3.5 by 2 mm, reddish brown

when dry, base cuneate, apex rounded; disc lobes rectangular, sometimes obtrapezoid, c. 0.15 by 0.2 mm, corners obtuse, membranous, glabrous, apex truncate; stamens 5, androphore c. 1 mm long, 5-cleft at top, filaments c. 0.5 mm long, anthers separate, oblong, c. 0.7 mm long. *Pistillate flowers* rare, c. 6–8 mm diam; pedicel 3.5–4 mm long, apically c. 0.8 mm thick, densely pubescent; sepals oblanceolate to oblong, 6–7 by 2–3 mm, foliaceous and accrescent in fruit, apex acute to acuminate, pubescent outside, especially near base and along midrib; petals not seen, fallen; disc lobes wide semi-orbicular or rectangular, c. 0.5 by 0.7 mm, slightly folded in the middle; ovary c. 1.5 mm diam, densely pubescent; styles not seen, fallen. *Fruits* and *seeds* not seen.

Distribution — Sumatra (endemic).

Note — This species is characterized by the glomerules subtended by 2 large, leaf-like bracts. Detailed locality of the type collection, *Korthals* '853', is based on Airy Shaw (1966).

10. Trigonostemon filiformis Quisumb. — Map 3

Trigonostemon filiformis Quisumb. (1930) 328, f. 7. — Type: M.S. Clemens 16751 (holo PNH†; iso A, NY*, UC*), Philippines, Luzon, Isabela Prov., Mt Moises.

Small trees; flowering branches 1.5–3.5 mm diam. *Outer bark* c. 0.1 mm thick, brownish to greyish, smooth, pubescent in young parts; inner bark c. 0.1 mm thick, reddish, sap light red; wood yellow or white. *Stipules* small, subulate, 0.5–1 mm long, pubescent. Leaves: petiole 1–3(–4.5) cm long, 0.6–1 mm diam, terete, sometimes angled, or furrowed above, pubescent; blade linear to long lanceolate, 13-22 by 0.8-1.5 cm, chartaceous, base acute to cuneate, with 2 adaxial, falcate glands, margin distantly serrate, teeth glandular, apex acuminate to caudate, upper surface dark green, glabrous, lower surface paler, softly appressed pubescent; midrib plain above and slightly raised and densely pubescent beneath, nerves obscure, 10-13 pairs, curved to almost right angled, connected, pubescent beneath, veins reticulate, very vague. Inflorescences terminal or axillary, racemes or thyrses (but often only 1 flower developed on each node); rachis slender, 2-6(-13) cm long, 0.15-0.4 mm diam, pubescent; bracts lanceolate or oblong, 2-10 by 0.3-1.3 mm, slightly pubescent. Staminate flowers: sepals obovate to round, c. 1.5 by 0.5 mm; petals c. 2 by 1.25 mm diam; disc unknown; stamens 3, anthers sessile, erect, globose. Pistillate flowers 3.5 (unopen)-7.5 (post-anthesis) mm diam; pedicels slightly thickened towards apex, 6-9 mm long, apically 0.8-1.1 mm diam, pubescent; sepals elliptic, 2.3-3 by 0.8-1.2 mm, accrescent to at least 9 by 2.2 mm, pubescent outside; petals oblong to oblanceolate, c. 4 by 1.25-1.5 mm, purple, glabrous; disc unknown; ovary at least 0.7 mm diam, densely pubescent; styles often indistinct, trifid; stigmas deeply bifid into 2 arms, each arm 0.6-1.2 mm long. Fruits and seeds unknown.

Distribution — Borneo (Sabah) and Philippines (Luzon). Habitat & Ecology — Lowland forest edge, ultramafic soil in Sabah. Flowering: April and December.

Notes — 1. The staminate flowers are not seen by us. The description is based on Quisumbing (1930).

- 2. The species is distinct from *T. verticillatus* var. *salicifolius* by the staminate flowers with 3 instead of 5 stamens. Another useful character is that *T. verticillatus* var. *salicifolius* often has two pairs of adaxial glands at leaf base, whereas *T. filiformis* always has one.
- 3. The type was collected from Mt Moises of the Philippines, as was the type of *T. stenophyllus* Quisumb. Both these two species are poorly known and probably they are conspecific, but this cannot be confirmed until further material is available of both species.

11. Trigonostemon flavidus Gagnep. — Map 4

Trigonostemon flavidus Gagnep. (1922) 749; (1925b) 320; P.T.Li & M.G. Gilbert (2008) 273. — Type: Harmand 3273 (holo P), Laos, in Lakhon mountains, near Me-Kong.

Trigonostemon heterophyllus Merr. (1930) 38; H.S.Kiu (1996) 163; Chantar. (2005) 24; (2007) 577, pl. 31: 1. — Type: W.T. Tsang 594 (= LU (Lingnan University) 17343) (A*, B*, BM, BO, ECON*, G*, K, L, MO*, NTUF*, NY*, P, PE, US, WIS*), China, Hainan, Danzhou County (Taam Chau District), Mt Sha Bao (Sha Po Shan).

Evergreen, small trees, 1-2.5 m tall; flowering branches up to 4 mm diam, grey, densely hirsute. Bark c. 0.3 mm thick, smooth or roughened; wood reddish brown. Stipules subulate, c. 0.7 mm long, hirsute around base. Leaves: petiole terete but sometimes flattened or grooved above, 0.2-1.2 cm long, densely hirsute; blade obovate or oblanceolate, sometimes unequal, unevenly narrowed in the lower middle part, 9–35 by 5–9 cm, thin chartaceous or membranous, base abruptly rounded, with 2 adaxial glands, margin distantly serrate, teeth small and nipple-like, apex caudate to acuminate, dark green above and dull light green underneath, hirsute on both sides, especially on nerves and margin; midrib thin, elevated on both sides, nerves 10-12 pairs, veins reticulate, often obscure. Inflorescences bisexual, cauline, usually in short cymes or thyrses, 1-3 cm long, hirsute, often bracteate under nodes or flowers; bracts lanceolate to linear, up to 4 by 0.6 mm. Staminate flowers c. 6 mm diam; pedicel c. 3.5 mm long, c. 0.2 mm thick, pinkish, glabrous; sepals elliptic or obovate, c. 2 by 1 mm, base connate, margin ciliate, apex acute, hirsute outside, glabrous inside; petals obovate, 4-4.5 by 2-2.5 mm, base claw-like, apex rounded, glabrous, dark reddish to maroon-purple; disc glands elliptic or obovate, c. 0.5 by 0.25 mm, narrowed at base and slightly reflected at apex, light orange, glabrous; stamens 3. androphore c. 1 mm long, c. 0.1 mm diam, shortly trifid at top, filaments c. 0.2 mm long; anthers free, divaricate at top, each theca 0.4-0.5 mm long, connective with apically numerous droplets with secretion. Pistillate flowers few, slightly enlarged when fruiting, up to c. 1 cm diam; pedicel (in fruiting flower) c. 7 mm long, thickened towards apex to up to 1 mm diam; sepals long lanceolate to linear, c. 2.5 by 1.2 mm when flowering, accrescent to up to 7.5 by 2 mm in fruit, margin with a few teeth, apex acuminate, outside hirsute, inside glabrous; petals not seen, fallen; disc glands rectangular to semi-orbicular, c. 0.5 by 0.4 mm, rounded or truncate at apex, glabrous; ovary c. 3.5 mm diam, bright dark green, densely hirsute, styles almost indistinct, stigmas 3, completely divided. Fruits c. 1.2 mm diam, green, densely hirsute; wall woody, c. 5 mm thick; columella c. 5 mm long. Seeds c. 6.5 by 5.5 mm, dark brownish when dry, hilum irregularly shaped, more or less triangular, c. 1.5 mm diam.

Distribution — India, China, Laos, Thailand, Malay Peninsula.

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

Note — *Trigonostemon flavidus* is tentatively treated as a separate species here, but it strongly resembles *T. semperflorens* from India, of which it might be a synonym. It differs by having more hairs on the upper leaf surfaces.

12. Trigonostemon hartleyi Airy Shaw — Map 1

Trigonostemon hartleyi Airy Shaw (1979) 535; (1980b) 206. — Type: Hartley 11087 (holo BRI*; iso L), Papua New Guinea, Morobe Dist., S of the Busu River, about 19 km N of Lae.

Small trees, up to 3.5 m tall; flowering branches terete, c. 3.8 mm diam, pale grey, young part appressed pubescent. *Outer bark* c. 0.1 mm thick, light grey, smooth; inner bark c. 0.1 mm

thick, reddish; sap clear, yellowish; wood whitish. Stipules subulate, c. 1 mm long, pubescent at base. Leaves clustered at apex of branchlets; petiole terete but grooved above, 1.5-3 cm long, c. 1.5 mm diam, glabrescent or appressed pubescent near base and apex when young; blade elliptic to obovate, 14-20 by 5-8 cm, thin chartaceous, base and apex acute, base with two adaxial glands, often subulate or nipple-like, margin subentire or slightly crenate or dentate, teeth falcate or often obscure, above dark green, underneath pale green glaucous, both sides glabrous or slightly pubescent when young; midrib flat above, raised beneath, nerves 7–9 pairs, veinlets reticulate, very thin and obscure. Inflorescences: staminate ones c. 2 cm long, fewflowered; primary rachis c. 1 cm long, c. 1 mm thick, glabrous, 2 bracts at apex, c. 1 mm long, subglabrous; secondary rachis 7 mm long, slender and glabrous, apex with few bracts; pistillate inflorescences axillary, often only one open flower present apically, with a few depauperate flowers below; peduncles terete, up to c. 9 cm long, c. 0.8 mm thick, glabrous or slightly pubescent at base, bracteate on each node; bracts lanceolate or triangular, c. 1 by 0.5 mm, pubescent outside. Staminate flowers: pedicel slender, 4-5 mm long; sepals distinctly unequal, wide elliptic or obovate, 1-2 mm long, apex rounded, with few hairs outside; petals wide ovate, c. 3 by 2 mm, orange, base shortly claw-like, apex rounded; disc lobes suborbicular, c. 0.5 mm diam, flat, erect, solid, glabrous, entire, brownish when dry; stamens 5, androphore c. 0.5 mm long, anthers relatively large, ovoid, c. 0.5 mm long, erect, connectives very short. Pistillate flowers c. 7.5 mm diam; pedicel c. 3.5 cm long, thickened towards apex, up to 1.5 mm diam, glabrous; sepals oblong, 1.5-2 by c. 1 mm, not accrescent, apex rounded, greenish, outside slightly pubescent, with one conspicuous gland in the middle; petals not seen, caducous; ovary c. 3.5 mm diam, c. 3 mm high, stigmas 3, very shortly recurved. Fruits 12–15 mm diam, smooth, brownish. Seeds not seen.

Distribution — New Guinea (Morobe district, endemic). Habitat & Ecology — Rainforest, growing on slope. Altitude: 150 m. Flowering and fruiting: January.

Note — Descriptions of the staminate inflorescences, staminate flowers and ovary are based on Airy Shaw (1979). Only known from the type, *Hartley 12211* (K, paratype) and a doubtful collections (*Hartley 9811*, K). The species is different from *T. apetalogyne* only by having 5 instead of 3 stamens (see also note under latter).

13. Trigonostemon laevigatus Müll.Arg. — Fig. 5; Map 5

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 (1972a) 346; Whitmore (1973) 135; Airy Shaw (1975) 203; (1978) 417; (1981) 355; (1983b) 47; Chantar. (2005) 25; (2007) 578, f. 93. — Lectotype (designated here): Motley 686 (holo K), Borneo, Bangarmassing. Syntype: Barter s.n. (K, barcodes K000959289, K000959290), Borneo.

Trigonostemon everettii Merr. (1912) 408; Pax & K.Hoffm. (1914) 408; Merr. (1923) 451; Airy Shaw (1983b) 46. — Type: FB (Everett) 7257 (holo PNH†; iso A), Philippines, Negros, Mt Silay.

Trigonostemon anomalus Merr. (1920) 569; (1923) 451. — Type: FB (Villamil) 22018 (holo PNH†; iso A, US), Philippines, Mindanao, Zamboanga District, Naganaga.

Trigonostemon laevigatus Müll.Arg. var. petiolaris Airy Shaw (1978) 417; R.I.Milne (1995a) 28, in key, 29, in key. — Type: S (Chai) 19224 (holo K; iso L, SAN, SING), Sarawak, Fourth Division, Simpang Tiga, Ulu Mayeng, Kakus.

Trigonostemon sp. nov., aff. chinensis Merr.: Jabl. (1963) 168. — Voucher: KEP (Strugnell) 20275 (K, KEP, SING), Malaya, Pahang, Ulu Gali Raub. See note.

Trigonostemon sp. nov., aff. *chinensis* Merr.: Jabl. (1963) 168. — Voucher: *van Steenis* 910 (BO, L, SING), Sumatra, Anambas Islands, Siantan Island, E of Terimpa. See note.

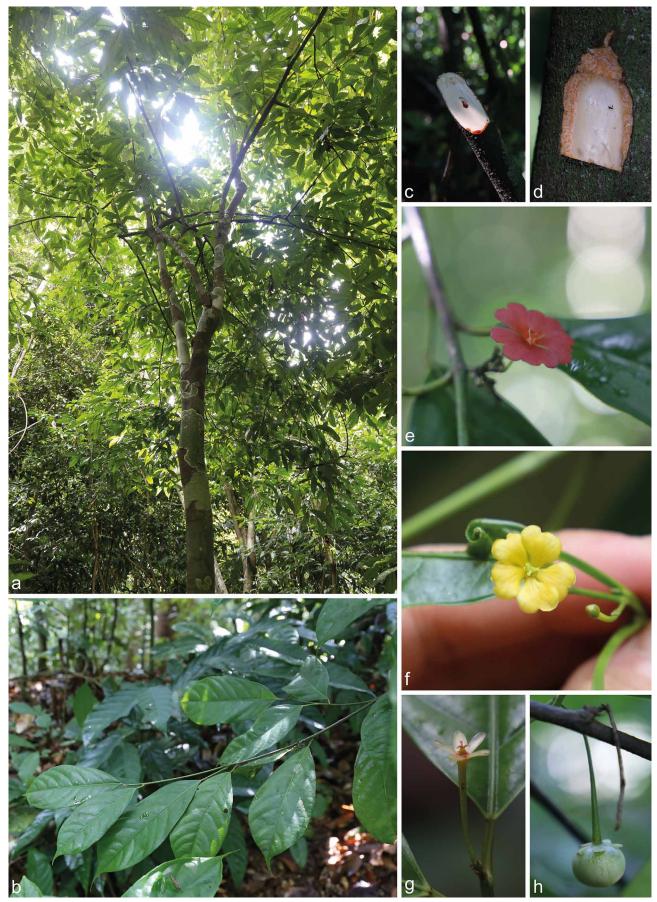
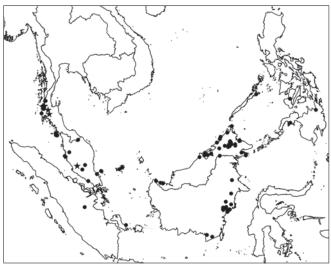


Fig. 5 Trigonostemon laevigatus Müll.Arg. var. laevigatus, from Kabili-Sepilok Forest Reserve, Sandakan, Sabah, Malaysia (a–e, g–h), and Kuala Belalong, Temburong, Brunei (f). a. Growing habit; b. leaves; c. reddish exude; d. bark and wood; e. staminate flower; f. pistillate flower; g. pistillate flower, petals fallen; h. fruit. — Photos by Ren-Yong Yu.

Trees, 5–15 m tall, stem up to 15 cm diam; flowering branches 1.5-2 mm diam, often slightly pubescent near nodes and apical buds. Bark 0.3-0.5 mm thick, smooth, lenticellate, light greenish to pale or dark brownish to blackish; sap red, pink or colourless; wood whitish to reddish brown, with brownish pink rays. Stipules falcate to nipple-like, 0.3-1 mm long, pubescent, caducous, often obscure or not seen. Leaves: petiole terete but often flat or grooved above, 0.5-1.5(-4) cm long, wrinkled, glabrescent to pubescent, base and apex sometimes pulvinate; blade elliptic, sometimes oblong, ovate or oblanceolate, 6-20 by 2.5-8 cm, chartaceous or coriaceous, base acute to cuneate, with 2 adaxial glands, margin entire, apex acuminate to caudate, above greenish, underneath pale green below, both sides glabrous; venation triplinerved, midrib elevated beneath, nerves 6-9 pairs, bow-shaped, narrowed along margin, veinlets reticulate, obscure. Inflorescences terminal or axillary, cymes or paniculate thyrses, abbreviated and condensed or elongated and lax, 0.5-4 cm long, often branched, glabrescent or pubescent, bracts long-triangular to linear, up to 3 by 1 mm, velutinous. Staminate flowers 6-10 mm diam; pedicel c. 1 cm long, c. 0.2 mm thick, scarcely pubescent; sepals oblong to obovate to orbicular, 2-4.5 by 1.8-2.5 mm, sometimes unequal, then outer 2 or 3 larger, imbricate, margin entire, apex rounded, yellowish green, often finely puberulent on both sides, outside also pubescent with longer hairs and sometimes with a subapical gland (var. croceus); petals flabellate and bilobed, each lobe 3-6 by 1.5-3 mm, yellow or reddish, glabrous, few parallel veins visible, base claw-like, apex notched to 1/3 to 1/2 of length and often with a small gland below the notch; disc annular, c. 0.5 mm high, glabrous, apex recurved; stamens 3, androphore 0.3-1.5 mm high, trifid at apex, filaments 0.2-0.5 mm long, anthers oblong, c. 0.8 mm long, yellow, free, base somewhat auriculate, not divaricate at apex. Pistillate flowers c. 6 mm diam, pedicel thickened towards apex, up to 2.5 cm long, apically c. 1 mm thick, slightly pubescent; sepals, petals and disc as in staminate flowers; ovary c. 1 mm diam, greenish, glabrescent to densely hairy, style c. 0.1 mm long, sometimes indistinct, stigmas 3 separate arms, c. 0.6 mm long, c. 0.1 mm thick, apex very slightly thickened and bifid. Fruits c. 1 cm diam, greenish, finely hairy; wall 0.4-0.6 mm thick, exocarp detaching; columella 5-6.5 mm long. Seeds 7-8 by 6-7 mm; hilum 1.5-3 by 1-2 mm.

Distribution — Vietnam, Thailand, Malay Peninsula, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands.



Map 5 Distribution of *Trigonostemon laevigatus* Müll.Arg. var. *laevigatus* (●) and *T. laevigatus* var. *croceus* (B.C.Stone) R.Y.Yu & Welzen (★).

Note — The species is wide-spread and is often recognized by its short petiole, hairy sepals, and often flabellate and bilobed petals. The last three synonyms are only tentatively treated here because of the inadequate material.

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 Fig. 5; Map 5

Sepals without a gland outside.

Distribution — As the species.

Habitat & Ecology — Mixed lowland dipterocarp forest, growing on clay to sandy soils to basalt derived soils of hill slopes. Altitude: 30–600 m. Flowering: all year round; fruiting: April, August, September, November.

Vernacular name — Borneo: Mampan (Banjar-Malay).

Notes — 1. The variety generally has a short petiole (often shorter than 1.5 cm) but it can be up to 4 cm long in some populations (e.g., in some populations from Brunei and Sabah). Since the variance is continuous, Airy Shaw's var. *petiolaris* is synonymised here.

2. The sepals often have 2 layers of hairs on the outside, the relatively stiffer and longer hairs form the upper layer and often a layer of very dense and fine hairs that forms the lower layer and which is also present on the inside.

b. var. croceus (B.C.Stone) R.Y.Yu & Welzen, comb. nov. & stat. nov. — Map 5

Trigonostemon croceus B.C.Stone (1980) 249. — Type: *Stone 9586* (holo KLU; iso K, L, PH*), Malaysia, Selangor, on the Pahang border at Genting Sempah.

Sepals with a gland outside.

Distribution — Thailand, Malay Peninsula.

Habitat & Ecology — Hill evergreen forest to grassy sites. Altitude: 900–1300 m. Flowering: November to May.

Note — Stone (1980) newly described *T. croceus*, because it had 5 instead of the 3 stamens of *T. laevigatus*. We dissected one staminate flower from the isotype and it turned out to have 3 stamens. Its only difference from the typical *T. laevigatus* are the showy, protruding glands on the sepals, but there is a continuous variation from being glandless to having a flat gland to even having a protruding gland. However, according to the specimen notes the *croceus* form occurs at higher altitudes than the typical *laevigatus* form. Therefore, *T. croceus* is here regarded as a variety of *T. laevigatus*.

Trigonostemon longifolius Wall. ex Müll.Arg. — Fig. 6; Map 6

Trigonostemon longifolius Wall. (ex Baill. (1858) 341, nom. inval., still nom. nud.) ex 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 (1972a) 347; Whitmore (1973) 136; Airy Shaw (1981) 355; Chantar. (2005) 26; (2007) 579, f. 94. — [Croton longifolius Wall., Numer. List (1847) 7717, nom. nud., non Müll.Arg. (1873) 170.] — Lectotype (designated here): Wallich 7717 (K, barcode K000959328; iso BR, G, GH, K, barcode K000959327), Malaya, Penang Island. Syntypes: Griffith KD 4797 (K), Malaya, Malacca; Griffith KD 4798 (K), India, Tenasserim and Andamans.

?Athroisma dentatum Griff. (1854a) 478 ('dentatis'); (1854b) pl. 585, f. 4. — Type: *Griffith s.n.*?, Nov. 1834 (K?), Mergue, 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?), Mergue, Tenasserim (see Airy Shaw 1972a: 347).

Croton longipedunculatus Elmer (1908) 311. — Trigonostemon longipedunculatus (Elmer) Elmer (1911) 1306; Pax & K.Hoffm. (1914) 408; Merr. (1923) 452; Airy Shaw (1983b) 47; R.I.Milne (1995a) 38. — Type: Elmer 7264 (holo PNH†; iso A, BO, E, G, K), Philippines, Leyte, Prov. of Leyte, Palo. Trigonostemon oblanceolatus C.B.Rob. (1911) 337; Pax & K.Hoffm. (1914) 407; Merr. (1923) 452; Airy Shaw (1983b) 47. — Type: Williams 2185 (holo PNH†; iso K, NY, US), Philippines, Mindanao, Zamboanga District, Say River

Prosartema gaudichaudii Gagnep. (1925a) 468, non Trigonostemon gaudichaudii (Baill.) Müll.Arg. (1865) 213. — Trigonostemon gagnepainianus Airy Shaw (1978) 415. — Syntypes: Gaudichaud 167 (P*), Vietnam, Tourane; Poilane 8306 (P*), Vietnam, from Nhatrang to Ninh Hoa; 10220 (P*), Vietnam, prov. de Quang Tri, Mai-lanh; Poilane 10446 (P*, K), Vietnam, Prov. de Quang Tri, Dent du Tigre.

Trigonostemon elmeri Merr. (1929) 162; Jabl. (1963) 162; Airy Shaw (1975) 202; R.I.Milne (1995a) 27, in key, 29, in key, 41. — Type: Elmer 20936 (holo PNH†; iso A, BISH*, BM, BO, BR*, CAS*, CM*, G*, HBG*, K, L 2 sheets, M*, MICH*, NY*, P*, PH*, S*, SING, U), Sabah, near Tawao.

Trigonostemon howii Merr. & Chun (1935) 262; H.S.Kiu (1996) 163. — Type: F.C. How 70940 (A*, IBSC*, K, NY*, US*), China, Hainan.

Trigonostemon ionthocarpus Airy Shaw (1968) 407; (1975) 203; R.I.Milne (1995a) 27, in key, 29, in key. — Type: SAN (Meijer) 19672 (holo K; iso BRI*, SING), Sabah, Sandakan Dist., Mile 17, Gum-Gum.

Trigonostemon matangensis R.I.Milne (1994) 445, f. 1; (1995a) 27, in key, 29, in key. — Type: Ridley s.n. (holo K), Sarawak (SW), 1st Division, Matang. Trigonostemon longipedunculatus (Elmer) Elmer var. mollis R.I.Milne (1995a) 27, in key, 29, in key, 40. — Type: SAN (James Ah Wing) 38218 (holo K; iso L, SAN), Sabah, Sandakan District, Sekong Kechil, Sepagaya, Sandakan Bay.

Trigonostemon sanguineus auct. non Gagnep.: Ridl. (1926) 80. — Trigonostemon ridleyi Jabl. (1963) 165, f. 8. — Type: Boden-Kloss 14697 (holo SING; iso K), Sumatra, Sipora Island of Mentawi Group.

Small trees, 1–5 m tall, stem up to 7 cm diam; flowering branches 2–5(–7) cm diam. *Outer bark* 0.1–0.25 mm thick, smooth, pubescent to hispid when young, whitish to brownish; inner bark 0.2–0.4 mm thick, yellowish to reddish brown, soft; sapwood 0.8–1.5 mm thick, white to dark brownish; heartwood 2–3 mm diam. *Stipules* linear to hook-like, 2–8.5 by 0.3–1 mm,



Fig. 6 Trigonostemon longifolius Wall. ex Müll.Arg., from Kabili-Sepilok Forest Reserve, Sandakan, Sabah, Malaysia (a), and Kuala Belalong, Temburong, Brunei (b-e). a, b. Growing habit; c. staminate flowers; d. pistillate flower; e. fruits. — Photos by Ren-Yong Yu.

often pubescent. Leaves: petiole terete, 0.4-3.5 cm long, often wrinkled, hispid; blade oblanceolate, (10-)12-28(-46) by (2.8-)4-10(-15) cm, membranous to chartaceous to coriaceous, base cuneate to round, margin distantly serrate, apex acuminate to slightly caudate, upper side glabrous to slightly pubescent, lower side often pubescent to hispid; midrib robust, elevated on both sides, nerves (9-)11-16(-33) pairs, often slightly curved and connected along margin, veins scalariform, veinlets reticulate. Inflorescences uni- or bisexual, axillary or terminal, loose or condensed, per node a single flower or short cymes, rachis (7-)15-30(-55) cm long, 0.5-4 mm diam, pubescent; bracts lanceolate to linear, 3-8 by 0.3-1 mm, pubescent. Staminate flowers 4-5 mm diam; pedicel 1.5 (Thailand, Malay Peninsula, Sumatra) – 5 (Borneo) mm long, 0.1 – 0.2 mm diam, pubescent, base articulate; sepals elliptic, 1.2-2 by 0.7-1 mm, green, margin entire, apex rounded, pubescent outside, glabrous inside; petals spathulate to obovate, 2-2.5 by 1.2-1.7 mm, pinkish to bluish black, base slightly claw-like, sometimes with 2 gland lobes (Thailand, Malay Peninsula, Sumatra), margin entire, apex rounded, smooth outside, often rough and papillose inside; disc annular, 0.2-0.4 mm wide, margin often 5-notched; stamens 3, androphore c. 0.4 mm long, trifid at top, anthers free, divaricate, connective sometimes protruding at top (Thailand, Malay Peninsula, Sumatra). Pistillate flowers 4-5 mm diam; pedicel slightly thickened towards apex, 1.7-3 (Thailand, Malay Peninsula, Sumatra)-9 (Borneo) mm long, apically 0.5-1 mm diam; sepals elliptic to lanceolate, 1.2-1.8 by 0.8-1.5 mm, margin entire, apex rounded to acute, pubescent outside, glabrous inside; petals and disc as staminate flowers; ovary c. 0.7 mm diam, densely pubescent, glabrescent, slightly (Thailand, Malay Peninsula, Sumatra, Borneo, Philippines) to extremely (Borneo) warty; styles short, often indistinct, trifid; stigmas bifid into 2 flattened lobes. Fruits 1.2-1.4 cm diam, green, pubescent, glabrescent, slightly to extremely warty; sepals persistent, not accrescent; wall 0.4-0.6 mm thick, exocarp partly splitting off; columella 5.5-6 mm long. Seeds 6.5–7 by 6–6.5 mm; hilum elliptic to rhombic to heart-shaped, 2-4.5 by 2.5-4 mm.

Distribution — China, India, Thailand, Vietnam, Malay Peninsula, Sumatra, Borneo, Philippines.

Habitat & Ecology — Primary to logged forests, flat land to hill sides, sometimes near rivers, growing on black soil or sandy or stoney clay. Altitude: 15–1000 m. Flowering and fruiting: all year round.

Map 6 Distribution of Trigonostemon longifolius Wall. ex Müll.Arg.

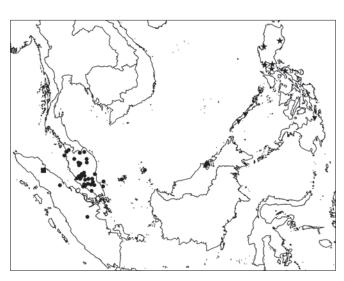
Notes — 1. The staminate flowers are cauliflorous on one specimen (*Wenzel 1513*, BM).

2. Most of the species in this complex, now synonymised, were based on slight differences, but all show the same essential similarities including the short petiole, spike-like inflorescences and the more or less warty fruits. All of these indicate that they are conspecific. Two kinds of forms can be distinguished, though there is overlap via intermediates that cannot be placed: a form, often identified as T. elmeri, mostly distributed in Thailand, Malay Peninsula, Sumatra and parts of Borneo with short pedicel (1.5–3 mm long), petals with 2 glands at base and densely hairy but slightly warty fruits; another form, often identified as T. ionthocarpus, mainly in parts of Borneo and the Philippines with longer but thinner pedicel (3-9 mm long), petals with papillate hairs inside but without a basal gland and sometime extremely warty fruits. A molecular phylogeny of this species complex may enlighten an infraspecific distinction between the forms.

15. *Trigonostemon longipes* (Merr.) Merr. — Fig. 7; Map 7

Trigonostemon longipes (Merr.) Merr. (1916b) 191; Pax & K.Hoffm. (1919) 41; Merr. (1923) 452; Airy Shaw (1983b) 47. — Dimorphocalyx longipes Merr. (1906) 82. — Lectotype (designated here): FB (Whitford) 1066 (lecto K; iso P), Philippines, Luzon, Bataan Prov., Mount Mariveles. Syntypes: FB (Borden) 1801 (BM, BO, K), Philippines, Luzon, Bataan Prov., Mount Mariveles; FB (Merrill) 2699 (BM, K), Philippines, Luzon, Province of Rizal, Rosphoso

Small trees, up to 4 m tall, stem c. 9 cm diam; flowering branches terete, 2-3 mm diam, glabrous except pubescent near apical buds. Bark c. 0.2 mm thick, pale brownish, smooth, wrinkled; wood pale yellowish. Stipules subulate, 0.5-1 mm long, pubescent. Leaves: petiole terete but grooved above, 1-8 cm long, glabrescent or slightly pubescent; blade oblong, sometimes oblanceolate, 5.5–16 by 2.5–6 cm, coriaceous, base cuneate, with 2 adaxial glands, margin entire or slightly crenate, apex acuminate to somewhat caudate, upper side dark green, lower side light green, both sides glabrous; midrib flat above and elevated underneath, nerves 8-11 pairs, curved and connected along margin, veinlets reticulate, often obscure. Inflorescences often unisexual, axillary or terminal, sometimes cauliflorous, thyrsoid, up to 15 cm long, glabrous or slightly pubescent, part of staminate flowers single and cauliflorous; few glomerules on a long main rachis, each node subtended by 1 bract; latter lanceolate, up to 1.5 by 0.8 mm, often pubescent; glomerules



Map 7 Distribution of *Trigonostemon longipes* (Merr.) Merr. (★); *T. lychnos* (R.I.Milne) R.Y.Yu & Welzen (▲); *T. magnificus* R.I.Milne (■ including also ●); *T. malaccanus* Müll.Arg. (●); *T. merrillii* Elmer (▼).

few-flowered (often 5–10 in staminate inflorescences and 1–3 in pistillate ones), bracteate under each flower, lanceolate, up to c. 0.7 by 0.5 mm, densely pubescent. *Staminate flowers* c. 4 mm diam; pedicel c. 1 mm long, c. 0.45 mm diam, slightly pubescent; sepals orbicular, c. 2 by 2 mm, imbricate, base connate, apex rounded, pubescent outside; petals elliptic, c. 2 by 1 mm, contort, margin sometimes ciliate; disc lobes obovate or semi-orbicular, c. 0.5 by 0.5 mm, c. 0.15 mm thick, glabrous, apex acute; stamens 5, androphore short, often indistinct, anthers c. 0.5 mm long, gathered on the top of androphore. *Pistillate*

flowers c. 6 mm diam; pedicel 2–3 mm long, thickened towards apex, c. 1.2 mm thick; sepals oblong, slightly accrescent in fruit, up to 3.5 by 2 mm, pubescent outside, apex rounded; petals not seen, caducous; disc lobes semi-orbicular, c. 0.5 by 1 mm, glabrous; ovary not seen. Fruits c. 1 cm diam, glabrous; wall c. 0.4 mm thick; columella c. 3 mm long. Seeds c. 6 mm diam.

Distribution — Philippines (endemic).

Habitat & Ecology — Secondary forest, on clay loam. Altitude: 175–250 m. Flowering: January to April, September; fruiting: January, April.



Fig. 7 Trigonostemon longipes (Merr.) Merr., cultivated in Makiling Botanical Garden, University of the Philippines-Los Baños, Laguna, the Philippines. a. Top view of the tree; b. bark and a cauliflorous staminate flower; c, d. inflorescences; e. fruit. — Photos by Mark Gregory Q. Rule.

Note — The altitude information is based on Merrill (1906). The ovary is probably glabrous because the fruits are glabrous. The species strongly resembles *T. verticillatus* var. *verticillatus* in the variable long petiole and the 5 stamens of the staminate flowers, but they are different in their inflorescences: several flowers (often more than 5) cluster into significant glomerules along the main rachis and the internodes are relatively distinct in *T. longipes* whereas in *T. verticillatus* var. *verticillatus* flowers are evenly spread along the spike-like rachis (only 1–3 flowers present per node) and the internodes are very short. A molecular phylogeny may result in a better conclusion about its distinctiveness.

Trigonostemon lychnos (R.I.Milne) R.Y.Yu & Welzen, comb. nov. & stat. nov. — Map 7

Trigonostemon polyanthus Merr. var. lychnos R.I.Milne (1995a) 28, in key, 30, in key, 35, f. 2. — Type: Coode 6766 (holo K; iso BRUN, K, KEP, L), Brunei, Tutong District, near Sungai Liang, Andalau Forest Reserve.

Slender treelets, up to 4 m tall, few branched; flowering branches c. 6 mm diam. Bark pale brownish, slightly pubescent near young parts, smooth when mature; sap red; wood reddish brown, pith loose. Stipules falcate, c. 1 mm long, caducous, pubescent. Leaves: petiole variable, 1-22 cm long (on a single flowering branch), terete, slightly grooved above, slightly pubescent when young, glabrous when mature; blade elliptic, 11-33 by 5.5-23.5 cm, chartaceous to coriaceous, base acute, with 2 adaxial glands, margin distantly serrate, teeth small, glandular, apex acuminate, upper side dark green (when dry), glabrous, lower side brownish (when dry), sparsely pubescent (more hairy on venations), more or less ciliate along margin; midrib slightly raised beneath, nerves 9-10 pairs, small veins reticulate. Inflorescences: staminate ones paintbrush-like, peduncle up to 13.5 cm long, bracts lanceolate, 1–1.6 by 0.5–0.7 cm; pistillate ones paintbrush-like but condensed into glomerules, pendulous; peduncles 20-29 cm long, 1.5-3.4 mm diam, terete, glabrous, base with 2 involucral bracts, as stipules, apex with few bracts subtending the glomerule, apical bracts obovate to lanceolate, 3-8 by 1.8-4.2 cm, base acute to reniform, apex acuminate, green, glabrous on both sides, glabrous or sometimes very sparsely pubescent near base; glomerules (few clustered short cymes) glabrous, with few small bracts under each flower, small bracts amorphous, slightly pubescent. Staminate flowers c. 4.5 mm diam, pedicel 4–7 mm long, very thin; sepals elliptic, c. 1.5 by 1 mm, pale pinkish green; petals long elliptic, c. 3 by 1.2 mm, purple; stamens 3, androphore c. 0.5 mm long, anthers with apically droplets on connective. Pistillate flowers unopen, pedicel covered by bracts, unseen; sepals elliptic, c. 3 by 2 mm; petals purple, elliptic, ovary unknown. Fruits and seeds unknown.

Distribution — Borneo (Belait and Tutong districts of Brunei, endemic).

Habitat & Ecology — Mixed lowland forest; heath forest on sandy soil (Milne 1995a). Altitude: 50 m. Flowering: April.

Vernacular — Sagubang Kayu (Brunei).

Note — A distinct species with only a few collections. We regard it as a separate species because of its big difference from T. polyanthus in the variable petiole and blade and the showy subtending bracts under the inflorescences. The variable petiole and leaf-like bracts also resemble T. villosus var. merrillianus.

17. Trigonostemon magnificus R.I.Milne — Map 7

Trigonostemon magnificus R.I.Milne (1995b) 51, f. 1 ('magnificum'). — Type: W.J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 19441 (holo K; iso BO, KLU, L, P*), Indonesia, Sumatra, Aceh, c. 75 km WNW of Medan, Gunung Leuser National Park, Sikunder Forest Reserve, Besitang River.

Erect small trees, up to 4.5 m tall; flowering branches 0.8–1 cm diam. Outer bark c. 0.1 mm thick, extremely wrinkled, densely tomentose; inner bark c. 1 mm thick, sap red, sticky; wood yellowish. Stipules subulate, c. 1 mm long, hirsute near base. Leaves: petiole 2.5–9 cm long, 1.7–3 mm diam, tomentellous, wrinkled; blade large, oblong, 18-35 by 7-14 cm, coriaceous, base truncate to acute, often with 2 adaxial subulate glands, margin entire or slightly distantly serrate, apex acuminate, upper side dull green, with a few hairs, lower side very pale, densely tomentose; midrib flat above, elevated and densely tomentose beneath, nerves 14-21 pairs, bow-shaped, veins and veinlets reticulate. Inflorescences bisexual, often axillary, very large panicles, up to 45 cm long, many-flowered, flowers open at same time, pilose; main rachis terete, sometimes angular, 1-2 mm diam, bracteate under each node, bracts linear, up to 8 by 1 mm; secondary and tertiary branches 0.3-0.6 mm thick, often with pistillate flowers above and more staminate flowers below. Staminate flowers small, 3-5 mm diam; pedicel 2.5-3 mm long, c. 0.2 mm diam, pubescent; sepals oblong or lanceolate, 1-2 by 0.5-1 mm, base connate, apex acute to acuminate, often with one globose gland outside, densely sericeous outside and scarcely puberulent inside; petals obovate, c. 3.5 by 1.5 mm, contort, base long cuneate, apex rounded, glabrous outside, rough and slightly papillose inside, dark purplish black; disc glands c. 0.4 by 0.4 mm, somewhat fleshy, apex often recurved; stamens 3, androphore erect, c. 0.8 mm high, anthers ellipsoid, c. 0.5 mm long, free, divaricate at apex. Pistillate flowers larger, c. 6 mm diam, more greenish; pedicel c. 4 mm long, 0.6-0.8 mm diam when flowering, thickened to 1.7 mm and elongated to 4 cm when fruiting, densely hirsutulous; sepals long-triangular or lanceolate, c. 2.5 by 1 mm when flowering, accrescent in fruit to 8.5 by 1.5 mm, with 3 teeth near apex and often with one gland on the tip of each tooth, densely hirsutulous on both sides; petals caducous, as staminate flowers; disc lobes semiorbicular, c. 0.3 by 0.5 mm, apex rounded, glabrous; ovary c. 2 mm diam, densely hirsute, styles very short, stigmas deeply bifid, arms linear, 1-1.5 mm long, often curved. Fruits c. 1.3 cm diam, densely covered with fine hairs, smooth; wall 0.5-0.8 mm thick, exocarp detaching; columella 6-7 mm long. Seeds c. 6 mm diam; hilum triangular, c. 2.8 by 1.7 mm.

Distribution — Sumatra (endemic).

Habitat & Ecology — Recently logged-over or marshy forests. Flowering and fruiting: August.

Note — A distinct but very rare species, known from two collections, the type and W.J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 19280, characterized by the tomentose indumentum, large and spreading inflorescences and sepals hairy on the inside.

18. Trigonostemon malaccanus Müll.Arg. — Fig. 8; Map 7

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. — Type: Griffith KD 4782 (holo K), Malaya, Malacca.

Small trees, up to 6 m tall, stem at least up to 5 cm diam; flowering branches up to 7.5 mm thick, glabrous or slightly pubescent in young parts, sometimes hollow. *Bark* c. 0.3 mm thick, smooth, brownish to greyish to blackish; sap clear or orange; wood pale yellowish. *Stipules* falcate or subulate, c. 1 mm long, often pubescent near base. *Leaves* clustered near apex of branches; petiole terete but grooved above, 2.5–22 cm long, sometimes thickened at apex or base, slightly pubescent, glabrescent; blade lanceolate, oblong or occasionally ovate, 10–25(–40) by 3–14 cm, chartaceous to coriaceous, base acute to rounded, with 2 adaxial, subulate or falcate glands, margin distantly serrate, teeth small, falcate or nipple-like, apex

acuminate to caudate, glabrous above, sparsely pubescent along venation beneath; midrib elevated and slightly pubescent (glabrescent in large leaves) on lower side, nerves 8-13 pairs, slightly curved and narrowed along margin, veinlets reticulate, often obscure. Inflorescences mainly unisexual, staminate ones thyrsoid, often terminal or subterminal, with short cymes along the main rachis, up to 25 cm long, densely hirsutellous, condensed when young; involucral bracts 2 or more, lanceolate to falcate, up to 2 by c. 0.5 mm; bracteate under cymes and under each flower, bracts lanceolate, up to 2 by 0.9 mm and 0.6 by 0.4 mm, respectively, hirsutulous; pistillate inflorescences racemose or thyrsoid, 1- or few-flowered cyme at each node, sometimes mixed with a few staminate flowers, up to 30 cm long, hirsutulous, condensed when young. Staminate flowers c. 4 mm diam; pedicel 1.5-2 mm long, 3-5 mm diam, hirsutulous; sepals orbicular to obovate, 1-2.1 by 0.6-1.6 mm, apex rounded, puberulent outside and often with a gland in the middle (on young flowers); petals obovate, c. 2.5 by 1.7 mm, pinkish or reddish purple, base cuneate, margin often wrinkled, apex rounded, glabrous on both sides; disc 0.6-1 mm diam, lobes obtrapezoid, c. 0.5 by 0.5 mm, c. 0.1 mm thick, glabrous, fused when young, separate and wrinkled when flowering, apex recurved and flat; stamens 3, androphore erect, c. 0.5 mm high, c. 0.2 mm diam, anthers free, long ellipsoid, c. 0.5 mm long. Pistillate flowers c. 4.5 mm diam; pedicel 1.5–2 mm long, 0.5–0.7 mm diam when flowering, slightly elongating to c. 4 mm long and 1 mm thick in fruit, hirsutulous; sepals and petals as staminate flowers, but petals caducous when fruiting; disc annular, margin irregularly undulate or with notches; ovary c. 1 mm diam, densely pubescent, style absent, stigmas deeply cleft for at least 3/4. Fruits c. 8 mm diam, puberulent, sepals persistent but not accrescent; wall 0.5-0.6 mm thick, exocarp detaching; columella 4.5-6 mm long. Seeds 5.5-6 by 5-5.5 mm; hilum triangular or heart-shaped, 2.5-3 by 2-2.5 mm.



Fig. 8 Trigonostemon malaccanus Müll.Arg., from Forest Research Institute Malaysia, Kepong, Malay Peninsula. a. Growing habit; b. leaves; c. pistillate inflorescence; d. leaf base with adaxial glands; e. pistillate flowers, petals fallen. — Photos by Ren-Yong Yu.

Distribution — Thailand, Malay Peninsula, Sumatra.

Habitat & Ecology — Evergreen forests to recently loggedover forests on hill ridges or in valleys, sometimes near rivers. Altitude: 100–850 m. Flowering: all year round; fruiting: June to August, November to February.

Vernacular name — Malay Peninsula: Putat.

Notes — 1. *Trigonostemon malaccanus* resembles *T. heteranthus* but has stubby staminate pedicels (often shorter than 2 mm, wider than 0.3 mm diam) rather than the slim pedicels of *T. heteranthus* (often longer than 2 mm and c. 0.1 mm diam), and entire pistillate sepals (vs fimbriate in *T. heteranthus*).

2. *Trigonostemon malaccanus* is also similar to *T. verticillatus* var. *verticillatus* but differs by having 5 instead of 3 stamens and the young inflorescences with distinct short and stiff hairs.

19. Trigonostemon merrillii Elmer — Map 7

Trigonostemon merrillii Elmer (1911) 1304; Pax & K.Hoffm. (1914) 407; Merr. (1923) 452; Airy Shaw (1983b) 47; R.I.Milne (1995a) 27, in key, 29, in key, 44. — Type: Elmer 12819 (holo PNH†; iso BISH*, BM, BO, F*, G*, HBG*, L, MO*, NY*, US*), Philippines, Palawan, Puerto Princesa (Mt Pulgar).

Shrubs, 2–3 m tall, stem up to 2.5 cm diam; flowering branches terete, up to 5 mm diam. Indumentum densely sericeous, especially on young parts. Outer bark 0.1-0.2 mm thick, pale brownish, hairy; inner bark 0.2-0.3 mm thick, reddish black, with sap; sapwood c. 0.4 mm thick, reddish brown; heartwood c. 2 mm diam, pale yellowish or brownish; pith empty. Stipules lanceolate to linear, 1-3 mm long, sericeous, caducous. Leaves: petioles terete or often angled, 1-2.5 cm long, densely sericeous; blade elliptic, 10-24 by 5-9.5 cm, chartaceous, base rounded or cordate, 2 adaxial glands present but often covered by silky hairs, margin distantly serrate, teeth often apiculate, falcate when young, apex acute to acuminate to caudate, upper surface greenish, paler beneath, both sides covered by long silky hairs; midrib slightly raised above and much elevated beneath, more densely sericeous, nerves 10-13 pairs, curved and connected near margin, veins and veinlets reticulate, sometimes obscure. Inflorescences: staminate ones thyrsoid with glomerulus along the main rachis, peduncle slender, 8-9 cm long and 0.4-0.7 mm diam, sericeous, with a few depauperate glomerulus below; involucral bracts subulate, at the base of inflorescences, c. 1.2 mm long, base hairy, bracts lanceolate, under each node, 1.1–3 mm long, sericeous; pistillate inflorescences racemose, main rachis slender, up to 12 cm long, c. 0.6 mm diam, sericeous; bracts as in staminate inflorescences. Staminate flowers 2.8-3.5 mm diam; pedicels c. 1 mm long, 0.15 mm diam, glabrescent; sepals unequal, elliptic to spathulate, 0.9–1.3 by 0.7–0.8 mm, narrowed near base, margin entire or slightly undulate, acute to rounded at apex, more or less pubescent outside; petals spathulate, 1.3–2.2 by 1.2–1.6 mm, dark purple, base cuneate, apex rounded, glabrous on both sides; disc cupular, slightly wrinkled, 5-toothed, each tooth rectangular, c. 0.2 by 0.2 mm, apex truncate, glabrous; stamens 3, androphore erect, 0.4-0.5 mm high, anthers ellipsoid, 0.25-0.35 mm long, gathered on the top of androphore, slightly divaricate at apex, connectives apically with some droplets (expanded cells) with secretion. Pistillate flowers unseen. Fruits c. 1.25 cm diam, glabrous; sepals not much accrescent. Seeds streaked or conspicuously mottled.

Distribution — Philippines (endemic).

Habitat & Ecology — Lowland dipterocarp forest. Altitude: 15 m. Flowering: March.

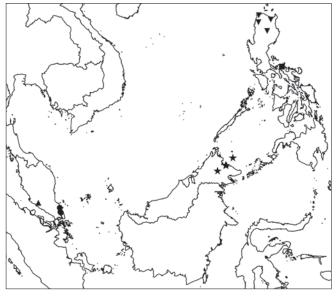
Note — The species resembles *T. oblongifolius* in the male inflorescences but differs from the latter by the blade being hairy on both sides. The description of fruits is based on Elmer (1911).

20. Trigonostemon oblongifolius Merr. — Map 8

Trigonostemon oblongifolius Merr. (1912) 409; Pax & K.Hoffm. (1914) 407; Merr. (1923) 452; Airy Shaw (1983b) 47. — Type: BS (Ramos) 13965 (holo PNH†; iso A, US), Philippines, Luzon, Prov. Cagayan, Abulug River. Trigonostemon luzoniensis Merr. (1920) 568; (1923) 452; Airy Shaw (1983b) 47. — Type: PNH (Ramos & Edaño) 33539 (holo PNH†; iso A, K), Philippines, Luzon, Camarines Prov., Paracale.

Small trees, up to 6 m tall; flowering branches terete, 2-4.5 mm diam, whitish and sparsely pubescent when young, buds densely golden pubescent. Bark c. 0.2 mm thick, smooth, pale brownish. Stipules subulate or falcate, 0.5-1 mm long, caducous, pubescent near base. Leaves: petiole terete but often grooved above, 0.5-3.5 cm long, more or less hirsute; blade oblong, 4-23 by 2-6.5 cm, coriaceous, base acute or rounded, margin often slightly recurved, apex acute, upper side paler (when dry), glabrous above and sparsely pubescent beneath; midrib often elevated and hirsute beneath, nerves 6-12 pairs, curved and often connected along margin, veinlets almost indistinct. *Inflorescences*: staminate ones (pre-flowered) paniculate thyrses, often axillary, at most few branched and with short glomerate cymes along the main rachis and the lateral branches, main rachis up to 18 cm long, 0.5-1 mm thick, slightly pubescent, bracteate under each branch, bracts lanceolate, c. 2 by 0.6 mm, hirsute outside; secondary branches often short, 0.5-1.5 cm long, cymes scorpioids, clustered, paintbrush- or broom-like, few-flowered, each flower bracteate; the latter lanceolate, up to 0.8 by 0.5 mm, hairy outside; pistillate ones (post-flowered, infructescences) racemose, axillary, c. 5 cm long, glabrescent; bracts lanceolate, c. 1.5 by 0.7 mm, glabrous. Staminate flowers (unopened) c.1.5 mm diam; pedicel c. 1 mm long, glabrous; sepals orbicular to ovate, c. 1.4 by 1.3 mm, imbricate, slightly hairy outside; petals ovate, c. 0.5 by 0.5 mm, glabrous; disc indistinct; stamens 3, androphore short, hidden, anthers gathered into a head on the top of androphore, c. 0.3 mm long. Pistillate flowers (fruiting): pedicel 2-2.2 cm long, thickened towards apex and scarcely hairy, sepals elliptic, c. 1.2 by 0.8 mm, outside sparsely pubescent near base; ovary villous; stigmas apically cleft, the lobes c. 0.5 mm long. Fruits c. 1 cm diam, appressed-hirsute, warty; wall c. 0.6 mm thick, exocarp partly splitting off; columella c. 5.5 mm long. Seeds c. 6 by 6.5 mm, dark brown; hilum heart-shaped, 2.5-3 by 1.5-1.8 mm.

Distribution — Philippines (Luzon, endemic). Habitat & Ecology — Flowering: January.



Map 8 Distribution of *Trigonostemon oblongifolius* Merr. (▼); *T. pentandrus* Pax & K.Hoffm. (♠); *T. polyanthus* Merr. (■); *T. rufescens* Jabl. (♠); *T. sandakanensis* Jabl. (★).

Note — The description of the ovary is based on Merrill (1912). The species has similar-looking inflorescences as *T. polyanthus*, but the main rachis is more distinct and the secondary rachis is much shorter and condensed than those of the latter species.

21. *Trigonostemon pentandrus* Pax & K.Hoffm. — Fig. 9, 10; Map 8

Trigonostemon pentandrus Pax & K.Hoffm. (1914) 406; Jabl. (1963) 164. — Type: Hubert Winkler 1792 (not traced), Malaya, Gunung Angsi near Sungei Gadub. Neotype (designated here): KEP FRI (R.Y. Yu) 86653 (holo L; iso KEP), Malaysia, Negeri Sembilan, Gunung Angsi.

Small trees, 1–2.5 m tall; flowering branches 5–7 mm diam, pith sometimes of loose tissue. *Outer bark* 0.2–0.25 mm thick, pale greyish, slightly fissured, glabrous; inner bark 0.15–0.4 mm thick, dark reddish to brownish, fibrous, sap orange; wood 0.5–0.6 mm diam, whitish to yellowish. *Stipules* subulate to

nipple-like, 0.5-1 mm long, glabrous. Leaves: petiole terete, 3.5-8 cm long, 2-3.2 mm diam, glabrous, thickened at base and apex, base somewhat sheathing; blade oblong, 23-35 by 6-9.5 cm, coriaceous, base cuneate, with 2 adaxial glands, nipple-like, showy, margin distantly serrate, teeth short-subulate, thickened, apex acuminate to caudate, upper side dark green, lower side pale green, both sides glabrous; venation penninerved, glabrous, midrib robust, slightly raised above and distinctly elevated beneath, nerves 14-16 pairs, straight, narrowed and branched and connected along margin, veinlets reticulate, often obscure. Inflorescences bisexual, (sub)terminal, short racemose, rigid, staminate flowers at top, pistillate flowers below, 2-6.5 cm long, rachis 1.3-2 mm diam, densely hirsutulous. Staminate flowers 6-7 mm diam; pedicel 2-3 mm long, 0.4-0.5 mm diam, pinkish red, hispidulous; sepals elliptic, 1.3-2 by 1-1.5 mm, white, base connate, margin entire or slightly irregularly undulate, ciliate, apex acute to rounded

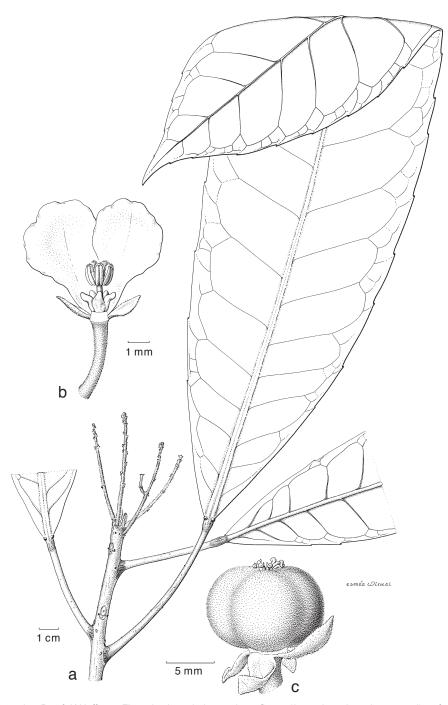


Fig. 9 Trigonostemon pentandrus Pax & K.Hoffm. a. Flowering branch; b. staminate flower (3 sepals and petals removed); c. fruits (all: Franck 1372, C). — Drawing by Esmée Winkel, 2016.

to emarginate, hirsutulous outside, glabrous inside; petals obovate, 3–4.2 by 2.5–3.2 mm, pink, base narrowed and somewhat claw-like, margin often wrinkled, apex bilobed, glabrous on both sides; disc lobes glandular, 0.6–0.7 by 0.3–0.6 mm, c. 0.15 mm thick, glabrous; stamens 5, androphore erect, 0.7–1 mm long, 0.2–0.3 mm diam near base, slightly narrowed above, 5-cleft at apex; anthers ellipsoid, 0.9–1 mm long, free, divaricate, connectives apically often with numerous dark reddish droplets (expanded cells) with secretion. *Pistillate*

flowers c. 0.3 mm diam (petals fallen); pedicel c. 1.7 mm long, articulated at base, c. 0.5 mm diam when flowering, slightly elongating in fruit to 3.5–4.5 mm long and c. 1.5 mm diam, hirsutulous; sepals elliptic to triangular, 2–2.8 by 1–1.2 mm, margin entire, ciliate, apex rounded to acute to acuminate, hirsutulous outside, glabrous inside; petals not seen, fallen; disc as staminate flowers; ovary c. 1.2 mm diam, reddish, densely hispid; styles indistinct; stigmas deeply fibid into 2 arms of 1.2–1.5 mm length, thickened at apex. *Fruits* c. 5.5 mm diam,

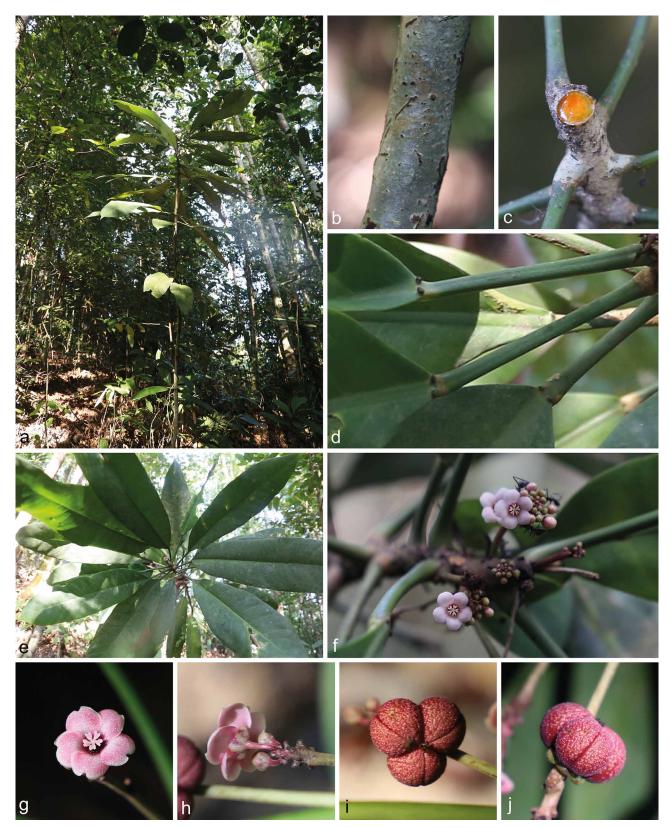


Fig. 10 Trigonostemon pentandrus Pax & K.Hoffm., from Gunung Angsi, Negri Sembilan, Malay Peninsula. a. Growing habit; b. bark; c. orange exude; d. leaf base with adaxial glands; e. top view of the tree; f. inflorescences, ants are potential pollinators; g, h. staminate flowers; i, j. fruits. — Photos by Ren-Yong Yu.

red in living plants, brownish when dry, densely hispid, sepals (slightly accrescent) and stigmas persistent; wall 0.4–0.5 mm thick, exocarp less than 0.1 mm thick, not detaching; columella c. 5 mm long. *Seeds* not seen.

Distribution — Malay Peninsula (Gunung Angsi, endemic). Habitat & Ecology — Flowering and fruiting: September to December.

Notes — 1. The species resembles *T. verticillatus* but a few unusual or unique characters make the species quite distinct: thicker leaves, one pair of showy blackish adaxial glands on leaves (glands not showy, but sometimes can be two pairs in *T. verticillatus*), shorter inflorescences and pinkish instead of reddish purple flowers.

2. The species has remained inadequately known and was only mentioned once (Jablonski 1963) since the original publication. The original type collection (*Hubert Winkler 1792*) is not

seen by us and is presumably lost, but our field observations and collections from Gunung Angsi (type locality) match the original description by Pax & Hoffman (1914) very well. We are strongly convinced that this is a good and distinct species. For more specimen citations, see Identification List.

22. Trigonostemon philippinensis Stapf — Fig. 11; Map 9

Trigonostemon philippinensis Stapf (1907) 206; Pax & K.Hoffm. (1911) 91; Merr. (1923) 452; Airy Shaw (1981) 355; (1983b) 47; R.I.Milne (1995a) 27, in key, 29, in key. — Type: Elmer 8326 (holo PNH†; iso BO, G*, K, L), Philippines, Luzon, Laguna Prov., Los Baños.

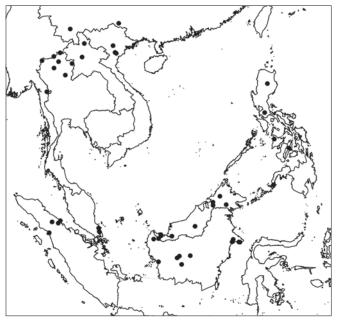
Trigonostemon thrysoideus Stapf (1909) 264 ('thyrsoideum'); Airy Shaw (1972a) 348; H.S.Kiu (1996) 166; Chantar. (2005) 29; (2007) 584, pl. 32: 1; P.T.Li & M.G.Gilbert (2008) 274. — Type: *Henry 11947* (A*, K, NY*), China, Yunnan, Simao (Szemao).

[*Trigonostemon paniculatus* Merr. ined., referred to by Jabl. (1963) 163 (as a synonym of *T. sumatranus* Pax & K.Hoffm.)].



Fig. 11 Trigonostemon philippinensis Stapf, cultivated in Xishuangbanna Tropical Botanical Garden, Yunnan, China. a. Growing habit; b. leaf; c. bisexual inflorescence; d. staminate flower; e. young fruit. — Photos by Roderick Bouman.

Trees or treelets, 6-15(-20) m tall, dbh 6-25(-40) cm, flowering branches up to 6.5 mm thick, brownish, glabrescent, slightly scaberulous basally. Outer bark hard, 0.5-1 mm thick, brownish to greyish, rugose, lenticellate; inner bark 2-5 mm thick, pinkish to reddish, brownish (when dry); exudate clear, pinkish; wood dirty pinkish white. Stipules falcate, sometimes linear, up to 1.5–2 by c. 0.4 mm, pubescent near base, caducous. *Leaves*: petiole terete, 1.5-15 cm long, 0.8-2.5 mm diam, glabrous or slightly pubescent, base in apical leaves often somewhat sheathing; blade elliptic to sometimes obovate, 10-31 by 4-13.5 cm, coriaceous, base acute or cuneate, with 2 adaxial falcate glands, margin distantly serrate to crenate, teeth subulate or falcate, apex acuminate to caudate, sometimes acute, dark green above, pale green beneath, both sides glabrous or with a few very scattered hairs; venation often slightly pubescent, midrib slightly raised above and raised beneath, nerves 8-14 pairs, curved, branched and connected along margin, veins and veinlets reticulate, obscure. Inflorescences often terminal, paniculate, much branched and many-flowered, up to 30 cm long (up to 15 cm long in the Philippines), usually unisexual to bisexual, finely pubescent; bracteate under each node, bracts triangular, 0.5-2.5(-5) by 0.2-1 mm (larger ones basal in inflorescence, smaller ones higher up; often longer in Thai and Vietnamese specimens), outside pubescent, inside glabrous, on large branches sometimes caducous and often with 2 falcate or subulate bracteoles at the sides (Sumatra and Borneo), up to 1 mm long. Staminate flowers c. 5 mm diam; pedicel 3.5-4 mm long, c. 0.2 mm thick, pubescent, articulate at base; sepals elliptic or somewhat obovate, 1.2-1.6 by 0.6-0.8 mm, pale greenish or greenish yellow, base narrowed and connate, margin somewhat translucent, apex rounded or slightly undulate, outside pubescent, often with a gland in the middle, inside glabrous; petals obovate to spathulate, 2.5-4 by 1.2-2 mm, base cuneate to claw-like, entire, apex rounded, yellowish, sometime pale cream inside and with a paler margin (Philippines), midrib and few parallel veins visible, glabrous; disc lobes trapezoid, 0.2-0.3 by 0.2-0.3 mm, c. 0.1 mm thick, fleshy, apex thickened, reflexed; stamens 3, androphore c. 0.5 mm long, free terminal part sometimes slightly trifid at top, sometimes bent (Sumatra and Borneo), anthers splitting off subapically from androphore, ellipsoid, c. 0.2 mm long, cream, divaricate (mainly in specimens from Thailand and Vietnam), connectives apically with droplets with secretion. Pistillate flowers of same size as staminate ones; pedicel 2.5-3.5 mm long,



Map 9 Distribution of Trigonostemon philippinensis Stapf.

apex slightly thickened, 0.6–0.7 mm thick; sepals and petals as in staminate flowers; disc lobes rectangular, c. 0.4 by 0.6 mm, apex truncate; ovary c. 1 mm diam, glabrous and warty, styles extremely short, stigmas with a shallow groove above. *Infructescence* pendulous, dull pale light green. *Fruits* c. 1.5 cm diam, greenish, glabrous, warty or aculeate above; pedicel 2.5–4 cm long, green; sepals persistent but not accrescent; wall woody, c. 0.6 mm thick, exocarp partly detaching; columella c. 0.8 cm long. *Seeds* 6–7.5 mm diam, dark brown when dry; hilum long-triangular to heart-shaped, 1–2.5 by 0.5–1.2 mm.

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

Habitat & Ecology — Lowland evergreen to deciduous forests, sometimes on limestone hills, near rivers; growing on red to yellow calcareous soils to granite bedrocks. Flowering and fruiting: all year round.

Notes — 1. The inflorescences are mainly unisexual because they generally consist of flowers of the same gender but sometimes are mixed with a few flowers of the other sex. The flowers can spread evenly along secondary rachis, whereby the whole panicle attains a pyramid-shape (Thailand and Vietnam), or the flowers cluster in brush- or broom-like groups on tertiary branches and the inflorescences seem more umbellate (Sumatra and Borneo).

2. Many collections (in many herbaria) of this species are incorrectly identified either as *T. sumatranus* or *T. paniculatus* (or '*T. paniculatum*') for a historical reason.

Pax & Hoffman's (1911) *T. sumatranus* was based on *Forbes* 2647 (BM, K, L), and is actually a synonym of *T. viridissimus*, a species that also bears paniculate inflorescences but can be easily distinguished from *T. philippinensis* by its much shorter petioles and stigmas being almost not bifid.

Merrill's *T. paniculatus* ('paniculatum') ined. was based on rich collections, which are actually *T. philippinensis*, but he never published this name, because he thought *T. paniculatus* could be the same as *T. sumatranus* (Jablonski 1963).

Jablonski (1963) never saw *Forbes 2647* and he misbelieved that *T. sumatranus* and *T. paniculatus* were conspecific, and therefore connected these two misperceptions, which explains these common misidentifications accordingly.

23. Trigonostemon polyanthus Merr. — Map 8

Trigonostemon polyanthus Merr. (1914) 492; (1923) 452; Airy Shaw (1983b) 48. — Type: BS (Ramos) 1645 (holo PNH†; iso BM, BO, BRI*, G*, GH*, L, NY*, P*, SING), Philippines, Samar, Cauayan Valley.

Trigonostemon diffusus Merr. subsp. condensus R.I.Milne (1995a) 47. — Type: PNH (Lagrimas et al.) 39433 (holo K; iso L, PNH†), Philippines, Luzon, Camarines Norte Province, Ilyang Binuauangan.

Shrubs, 2-3 m tall; flowering branches terete, 1.5-3 mm diam, slightly pubescent when young. Outer bark c. 0.1 mm thick, pale greyish, smooth; inner bark c. 0.1 mm thick, reddish brown; wood pale red or yellow. Stipules subulate or falcate, 0.5-1 mm long, pubescent. Leaves: petiole 0.8-3.2 cm long, pubescent, sometimes thickened at apex and base; blade elliptic, 4-15 by 2-4.5 cm, membranous or chartaceous, base truncate to rounded to acute, often with 2 adaxial falcate glands, margin entire or slightly distantly serrate, apex acuminate, upper surface glabrous, lower surface glabrescent to scattered pubescent; venation penninerved, slightly pubescent on lower side, midrib slightly raised above and elevated beneath, nerves 5-9 pairs, bow-shaped, connected along margin, veins and veinlets reticulate, often obscure. Inflorescences axillary, staminate ones paniculate thyrses, pubescent, main rachis up to 10 cm long, along secondary rachises (or tertiary rachises) scorpioid cymes, paintbrush-like and many-flowered, bracts

linear to triangular, 0.5–5 by 0.2–0.5 mm, pubescent outside; pistillate inflorescences cymose, 1- or few-flowered near apex and with few depauperate flowers below, peduncles c. 3 cm long, pubescent, bracts as staminate ones. *Staminate flowers* c. 4 mm diam; pedicel 2.5–3.5 mm long, c. 0.2 mm thick, pubescent; sepals elliptic, 1.2–1.6 by 0.3–0.6 mm, pubescent outside, margin sometimes slightly ciliate, apex acute to rounded; petals obovate to spathulate, 2.5–3 by 1–1.3 mm, base cuneate, margin entire, apex rounded, dark purplish and with one yellow or red flame-like honey mark in the lower middle part, glabrous, smooth; disc lobes oblong to trapezoid, c. 0.3 by 0.2 mm, c. 0.1 mm thick, apex acute or obtuse, glabrous; stamens 3, androphore erect, c. 0.5 mm long, anthers clustered at top of androphore, ellipsoid, c. 0.5 mm long, connectives apically with numerous droplets (or expanded cells) with secretion. *Pistil*-

late flowers c. 5.5 mm diam; pedicel slightly thickened towards apex, c. 4 mm long, apically c. 0.7 mm diam, sericeous; sepals oblong or lanceolate, 3.5–4.5 by 1–1.2 mm, margin sometimes with a few teeth, apex acute to acuminate, sericeous outside, often sparsely sericeous inside; petals as staminate flowers but larger, 4–4.5 by 1.5–2.7 mm; disc lobes semi-orbicular, c. 0.5 by 0.5 mm, apex rounded to acute; ovary c. 0.9 mm diam, densely pubescent, styles indistinct, stigmas c. 0.7 mm long, deeply bifid into 2 arms, each arm c. 0.55 mm long, thickened abaxially, base horseshoe-shaped. *Fruits* and *seeds* not seen.

Distribution — Philippines (Samar and Luzon). Habitat & Ecology — Flowering: April to June.

Notes — 1. A distinct species with paintbrush-like staminate inflorescences. Only 2 specimens present, the type specimen from Samar and *PHN (M. Lagrimas et al.)* 39433 from Luzon.



Fig. 12 Trigonostemon rufescens Jabl., from Mawai, Johor, Malay Peninsula. a. Growing habit; b. top view of a branch; c. leaf base with a hispid petiole and two adaxial glands; d. bark; e. red exude; f. staminate flower; g. fruit. — Photos by Ren-Yong Yu.

- 2. Milne (1995a) wrongly cited *PNH* (*Ramos*) 42686 as type of *T. polyanthus* (but later corrected this in an erratum via a printed sheet among the specimens), as it is not the type and actually belongs to *T. villosus*. Therefore, the reference of Milne (1995a) is not listed under *T. polyanthus*.
- 3. The holotype for *T. diffusus* subsp. *condensus* cited by Milne (1995a), *PHN* (*M. Lagrimas et al.*) 39437, might be a misprint as it should be *PHN* (*M. Lagrimas et al.*) 39433 (same date and place as 39437). He also cited *BS* (*Ramos*) 1645 as a paratype, but he probably did not notice that it was the type of an older name *T. polyanthus*. Although *T. diffusus* shares some similarity with *T. polyanthus* in the inflorescences, the differences are also striking and necessitate that both species are kept distinct, e.g., the inflorescences of *T. diffusus* are more elongated, diffuse and paniculate with a relative clear main rachis in the middle (*PNH* (*M. Lagrimas et al.*) 56725) and much longer internodes, and the pedicels are glabrous and thinner. Both species are relatively rare, more collections are desired.

24. Trigonostemon rufescens Jabl. — Fig. 12; Map 8

Trigonostemon rufescens Jabl. (1963) 152, f. 2; Whitmore (1973) 135. — Type: SFN (Corner) 29428 (holo SING; iso A*, BO, K, L, SAN, SING), Malaysia, Johore, 13.5 miles on Mawai – Jemaluang Road.

Small trees, up to 3 m tall; flowering branches 4-6 mm diam. Indumentum of densely golden hispid hairs. Outer bark c. 0.1 mm thick, dark brownish, hispid; inner bark c. 0.1 mm thick, blackish, sap red; sapwood 0.85-1 mm thick, whitish to pale yellowish; heartwood 2.6-2.8 mm diam, pale brownish, often hollow. Stipules subulate, c. 1 mm long, densely hispid, caducous. Leaves: petiole subterete, more or less furrowed above, 2-13 cm long, hispid; blade oblong to oblanceolate, 18-32 by 5-12 cm, coriaceous, base cuneate, acute to rounded or narrowly cordate, 2 adaxial glands often present, margin very distantly serrate, teeth subulate, apex acuminate to aristate, densely golden hispid on both sides; midrib flat above and elevated beneath, with two layers of hairs, soft pilose and hispid, nerves 11-14 pairs, curved and narrowed near margin, veins reticulate, often obscure above and distinct beneath. Inflorescences: staminate ones racemes or glomerules, 2–9 cm long, hispid; bracts lanceolate or linear, 8-20 by 1-5 mm, hispid; pistillate inflorescences racemose, up to 6 cm long, axillary, few-flowered (often only the top one develops), hispid; bracts as staminate ones. Staminate flowers c. 6 mm diam; pedicel at least 3.5 mm long, c. 0.4 mm diam, sparsely hirsutulous; sepals oblong, at least 3 by 1.2 mm, villose outside, glabrous inside; petals obovate or oblong, 3.5-5.5 by 1.5-2.2 mm, dark reddish, both sides glabrous; disc lobes elliptic, c. 0.4 by 0.4 mm, apex acute, glabrous; stamens 5, androphore erect, c. 1.5 mm long, 5-cleft at top, filament 0.3-0.4 mm long, anthers free, divaricate at top into two lobes, each lobe 0.65-0.8 mm long. Pistillate flowers c. 1.2 cm diam; pedicel c. 6.5 mm long, c. 0.7 mm diam, hispid; sepals lanceolate, 5.5-6.6 by 1.5-2.5 mm, apex acuminate, densely hispid outside, sparsely hispid inside; petals elliptic, c. 4.5 by 2 mm, margin wrinkled and irregular, apex near acute, glabrous on both sides; disc lobes rectangular to semi-orbicular, c. 0.4 by 0.8 mm, glabrous; ovary c. 1.3 mm diam, glabrous, evenly narrowed at top, styles c. 0.3 mm long, stigmas c. 1 mm long, bifid to middle. Fruits (immature) c. 7 mm diam, pinkish, pedicel c. 1 cm long, c. 2 mm diam (top); persistent sepals triangular, 1.2–1.5 by 0.6 mm. Seeds not seen.

Distribution — Malay Peninsula (Mawai – Jemaluang Road, endemic).

Habitat & Ecology — In drier part of swamps and on dry hill rocks. Flowering: February, May.

- Notes 1. This is a densely hairy species but the ovary turns out to be completely glabrous in our dissection, which is different from Jablonski's (1963) original description.
- 2. It is only known from its type locality where most of the forests have been replaced by oil palm plantations and the species, resampled in 2016 by the first author, is now extremely threatened.

25. Trigonostemon sandakanensis Jabl. — Fig. 13; Map 8

Trigonostemon sandakanensis Jabl. (1963) 159, f. 5, 6; Airy Shaw (1975) 204; R.I.Milne (1995a) 27, in key, 30, in key. — Type: SAN (Wood) 16018 (holo SING; iso BO, BRI*, K, KEP, L, SAN, SING), British North Borneo [Sabah], Kabili-Sepilok Forest Reserve, 15 miles W of Sandakan, Compartment 10.

Small trees, up to 5 m tall; barely branching, main branch occasionally with adventitious roots; flowering branches c. 1.2 cm diam. Outer bark dark brownish, slightly wrinkled; inner bark brown, sap red; sapwood pale yellowish; heartwood white. Stipules not seen, caducous, scars 0.5-0.6 mm diam. Leaves clustered at the end of branchlets; petiole less than 1 cm long, often lignified and somewhat sheathing; blade oblanceolate, large, 35-45 by 9-13 cm, coriaceous, base cuneate, evenly narrowing into the petiole, margin distantly serrate, teeth subulate, apex caudate, acuminate, apiculate or notched, dark green above, dull and pale green beneath, both sides sericeous; midrib slightly raised on both sides, robust, pubescent and velutinous, nerves 30-40 pairs, curved and more or less connected near margin, veins scalariform, veinlets reticulate, often obscure. Inflorescences: staminate ones subterminal, thyrsoid, short cymes on each node, main rachis erect, up to 20 cm long, sericeous; bracts linear or narrowed lanceolate, up to 7.5 by 1 mm, apex acuminate, abaxially sericeous; pistillate inflorescences racemose, almost spike-like when young, c. 5 cm long when flowering, up to 20 cm long when fruiting, densely sericeous. Staminate flowers 6-10 mm diam; pedicel 5-8 mm long, c. 0.2 mm diam, slightly hairy; sepals elliptic, 2-3 by 1.5-2 mm, apex rounded, reddish, glabrous on both sides; petals linear, 8-9 by 1.2-1.6 mm, margin often reflexed, apex acute, pinkish or pale purplish, outside smooth, inside rough, somewhat papillate and with numerous small and short, generally longitudinal ridges; disc annular, c. 1.6 mm diam, c. 0.4 mm wide, fence-like because of c. 20, apically undulate lobes; stamens 5, androphore erect, 0.6-1 mm long, pubescent at base, anthers clustered at top of androphore, ellipsoid, c. 0.7 mm long, thecae orange and connectives blackish when dry, thickened, protruding and often with few expanded cells apically. Pistillate flowers of same size as staminate ones; pedicel c. 7 mm long, apically c. 0.8 mm diam, elongating in fruit to up to 4 cm long, apically c. 1.5 mm diam, densely sericeous; sepals, petals and disc as staminate flowers; ovary c. 1 mm diam, densely sericeous, style c. 0.2 mm long, stigmas c. 0.7 mm long, bifid into 2 slightly thickened arms, each arm c. 0.5 mm long. Fruits c. 1 cm diam, hirsute, sepals persistent but not accrescent; wall c. 0.7 mm thick, exocarp partly detaching; columella 5-6.5 mm long. Seeds 7-7.5 mm diam; hilum rhombic, 3-4 by 2.5-3.5 mm.

Distribution — Borneo (Sabah, endemic).

Habitat & Ecology — Primary forest, near stream. Altitude: 5–20 m. Flowering: April to June; fruiting: December.

Note — A unique species only known from the Kabili-Sepilok Forest Reserve in Sandakan, Sabah. The petals are linear and the inner surface is very rough and scurfy.



Fig. 13 Trigonostemon sandakanensis Jabl., from Kabili-Sepilok Forest Reserve, Sandakan, Sabah, Malaysia. a. Growing habit; b. adventitious root on the main branch; c. red exude. — Photos by Ren-Yong Yu.

26. *Trigonostemon scopulatus* R.Y.Yu & Welzen, *sp. nov.* — Fig. 14; Map 10

This species resembles *T. villosus*, but there are two kinds of inflorescences, those on the leafless parts are contracted and those in the axils of still present leaves are elongated and have the flowers especially in the upper part and may resemble brooms, the ovary is glabrous. — Type: *KEP FRI (P.F. Cockburn) 7859* (holo L; iso K, KEP, SING), Malaysia, Johore, Ulu Endau, Labis FR, Compt. 277. Paratypes: *KEP FRI (F.S.P. Ng) 5207* (KEP, L), Malaysia, Johore, Mersing, Arong FR, Compt. 90; *Joseph Lai & Ali Ibrahim LJ 22* (SING), Singapore, Mandai Forest, next to Mandai Columbarium; *Joseph Lai & Ali Ibrahim LJ 80* (SING), Singapore, Mandai, Central Catchment Nature Reserve.

Small trees, up to 3 m tall; flowering branches c. 3.5 mm diam, sometimes hollow. *Outer bark* 0.1–0.2 mm thick, dark brownish, tomentellous; inner bark 0.1–0.3 mm thick, dark reddish to blackish; sapwood 1.5–2 mm thick, brown; heartwood

c. 1.5 mm diam, brown. Stipules subulate, c. 0.5 mm long, often covered with hairs. Leaves: petiole terete, 2.5-12 cm long, hispidulous; blade oblong, 12-26 by 4-7.5 cm, chartaceous, base narrowly cordate, glands not seen, margin entire or slightly, distantly serrate, apex acuminate, upper side dark brownish to black (when dry), glabrous, lower side brown (when dry), papillate-hispid; venation penninerved, papillose hispid on lower side, midrib flat above and elevated beneath, nerves 10-13 pairs, straight or slightly curved, branched and connected along margin, veins scalariform, veinlets reticulate. Inflorescences bisexual, in the leafless parts fascicled, in the axils of still present leaves elongated and racemose or thyrsoid, with the flowers concentrated at the upper part of the rachis and broom-like, rachis up to 10 cm long, 0.8-1 mm diam, densely hispid; bracts lanceolate, 4–5 by 0.6–1.2 mm, apex acuminate, densely hispid outside, glabrous inside. Staminate flowers

2.5–3.5 mm diam; pedicel 4.5–5.5 mm long, 0.2–0.3 mm diam, hispidulous; sepals lanceolate to linear, 1–1.5 by 0.2–0.3 mm, margin entire or slightly serrate, apex acuminate, outer surface hispid and with few whitish oil-like spots; petals elliptic, 1.2–1.5 by 0.7–0.8 mm, dark red to purple, glabrous on both sides; disc lobes rectangular to obtrapezoid, c. 0.2 by 0.2 mm, apex truncate, often slightly revolute; stamens 3, androphore c. 0.4 mm long; anthers gathered on the top of androphore, ellipsoid, c. 0.5 mm long. *Pistillate flowers* 0.45–0.5 mm diam; pedicel 6–8 mm long, 0.4–0.5 mm diam, densely hispid; sepals lanceolate, 2.5–3 by c. 0.5 mm, margin entire, apex acuminate,

hispid outside, glabrous inside; petals elliptic, 2.4–3 by 1–1.5 mm, dark red, margin entire, base and apex acute, glabrous outside, rough and slightly papillate inside; disc obtrapezoid, c. 0.45 by 0.45 mm, apex truncate; ovary c. 0.8 mm diam, glabrous; styles short, sometimes indistinct, c. 0.1 mm long; stigmas deeply bifid, arms 0.6–0.7 mm long, bent, thickened abaxially and sagittate near base. *Fruits* and *seeds* unknown.

Distribution — Malay Peninsula (endemic, only found in Johor, Malaysia and Singapore).

Habitat & Ecology — Disturbed forest near logging road; moist gully. Altitude: low. Flowering: March.

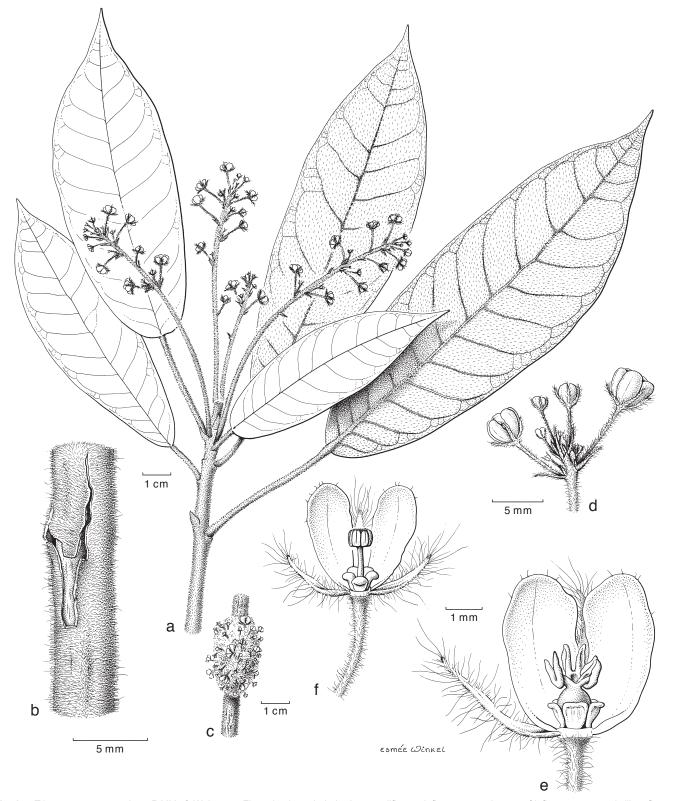
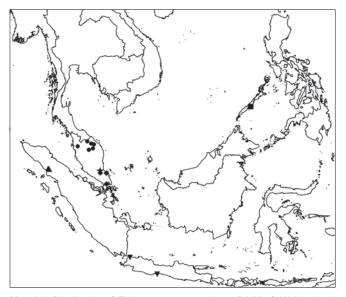


Fig. 14 Trigonostemon scopulatus R.Y.Yu & Welzen. a. Flowering branch; b. bark; c. cauliflorous inflorescence; d. apex of inflorescence; e. pistillate flower (3 sepals and 3 petals removed); f. staminate flower (2 sepals and 3 petals removed) (all: KEP FRI (P.F. Cockburn) 7859, L). — Drawing by Esmée Winkel, 2016.

27. Trigonostemon serratus Blume — Map 10

Trigonostemon serratus Blume (1825) 600 ('serratum'); Müll.Arg. (1866) 1110; Pax & K.Hoffm. (1911) 92; Backer & Bakh.f. (1963) 495; Airy Shaw (1982) 36. — Lectotype (designated here): Blume 1648 (L, barcode L.2258717; isolecto L, barcodes L.2258713, L.2258714, L.2258716), Java, Nusa Kambanga.

Small trees; flowering branches terete, 2-3 mm diam, buds densely sericeous. Outer bark c. 0.1 mm thick, with reddish stripes on which pubescence near apex, becoming pale greyish or brownish and smooth when mature; inner bark c. 0.1 mm thick, blackish; wood pale brownish. Stipules triangular to subulate, 0.4-0.7 mm long, sericeous. Leaves clustered at the end of branchlets; petiole obtriangular and flat to slightly grooved above, 1-3 mm long, often glabrescent, lower side rounded and pubescent; blade oblanceolate or oblong, sometimes slightly asymmetric, 6-20 by 2.5-6 cm, membranous, base obtuse to cordate, without glands, margin distantly serrate, teeth falcate, apex acuminate or caudate, glabrous above, paler and more or less pubescent beneath; midrib slender, slightly raised on both sides, nerves 7–15 pairs, connected along margin, veinlets reticulate, obscure. Inflorescences bisexual, axillary, racemes, bracts to rachis stipule-like, main rachis 3–6 cm long, 0.25–0.5 mm diam, slightly pubescent, bracts lanceolate to oblong to linear, 1-2.8 by 0.3-0.5 mm, pubescent. Staminate flowers c. 4 mm diam; pedicel c. 2 mm long, c. 0.2 mm thick, pubescent; sepals oblanceolate or ovate, c. 1 by 0.6 mm, margin entire, ciliate, apex acute, outside pubescent; petals obovate, c. 1.8 by 1 mm, margin sometime ciliate, apex rounded, outer surface glabrous, inner rough and papillate; disc lobes semi-orbicular, c. 0.3 by 0.5, apex rounded; stamens 3, androphore c. 0.5 mm long, anthers free, ellipsoid, c. 0.5 mm long, opening yellowish, connectives dark reddish (when dried), with numerous droplets with secretion. Pistillate flowers c. 3.5 mm diam; pedicel slightly thickened towards apex, c. 4 mm long, apically c. 0.7 mm diam, accrescent when fruiting to up to 9 mm long and 1 mm diam, pubescent; sepals lanceolate, 1-1.5 by 0.5-0.7 mm, margin sometimes serrate, teeth glandular, apex acute, pubescent outside; petals as staminate flowers but caducous and slightly larger, 2-2.5 by 1-1.5 mm; disc lobes semi-orbicular, c. 0.55 by 0.45 mm, thin membranous, apex acute or rounded; ovary c. 0.8 mm diam, densely sericeous, style c. 0.1 mm long, almost indistinct, stigmas c. 0.5 mm long, completely bifid. Fruits c. 8 mm diam, finely pubescent; columella c. 4 mm long. Seeds not seen.



Map 10 Distribution of *Trigonostemon scopulatus* R.Y.Yu & Welzen (♠); *T. serratus* Blume (▼); *T. sinclairii* Jabl. (♠); *T. victoriae* R.Y.Yu & Welzen (♠); *T. wetriifolius* Airy Shaw & Ng (★); *T. wildeorum* R.Y.Yu & Welzen (♠).

Distribution — Java (endemic). Habitat & Ecology — Rainforest. Flowering: November.

Note — The young branches are reddish (in dried specimens) and pubescent. The outer bark regularly sheds off, and reddish stripes remain. In older parts the branches become pale greyish or brownish.

28. Trigonostemon sinclairii Jabl. — Map 10

Trigonostemon sinclairii Jabl. (1963) 154, f. 3, 4; Whitmore (1973) 135. — Type: SFN (Sinclair & Kiah bin Salleh) 40418 (holo SING), Malaya, Terengganu, Block 3B Gunong Tebu F.R., 51st mile Kuala Terengganu – Berut Road.

Shrubs or small trees, up to 5 m tall, stem sparsely branched, flowering branches 0.8-1.3 mm diam. Indumentum often of 2 layers of simple hairs, shortly villose and longer papillate-hispid. Outer bark 0.1–0.2 mm thick, often fissured, yellowish to brownish, villose and papillate-hispid; inner bark c. 0.5 mm thick, fibrous, dark brownish to blackish, with sap; sapwood 0.2-0.3 mm thick, yellowish to reddish brown; heartwood 0.4-0.7 mm diam, brownish. Stipules subulate, c. 1 mm long, caducous, often not seen. Leaves: petiole 4-15 cm long, villose and hispid; blade oblong, 20-45 by 8-17 cm, coriaceous, base obtuse or slightly cordate, with 2 adaxial glands, latter falcate or subulate, but often covered by long hairs, margin entire, often papilloseciliate, apex acute to acuminate, or sometime rounded, both sides papillate-hispid; midrib raised and densely villose and hispid on both sides, nerves 15-20 pairs, slightly raised on both sides, curved and narrowed near margin, with two layers of hairs, villose and papillate-hispid, veins scalariform, papillatehispid (only one layer, not villose), veinlets reticulate, obscure above. Inflorescences: staminate ones axillary, raceme-like thyrses, rachis up to 25 cm long, densely villose but sparsely hispid; bracts linear, 6–12 by 0.7–1 mm, hispid; pistillate inflorescences axillary, racemose, or sometimes sparsely branched at bottom, rachis sometimes hollow, up to 40 cm long, villose and hispid; bracts as staminate inflorescences, but larger, up to 20 by 2 mm. Staminate flowers c. 7 mm diam; pedicel 0.5–0.8 mm long, 0.2-0.4 mm diam, sparsely hispid; sepals lanceolate, 1.5-2 by 1-1.5 mm, apex acute, outside hispid and with a gland near apex, inside glabrous, sometimes with a few pale pustules on both sides; petals elliptic, c. 4.8 by 2.5 mm, base rounded, apex acute to rounded, dark reddish, contort, glabrous to often with sparsely pale pustules on both sides; disc glands rhomboid, 0.5-0.7 by 0.4-0.65 mm and c. 0.2 mm thick, apex acute, occasionally with sparsely pale pustules; stamens 3, androphore erect, c. 0.6 mm long, anthers ellipsoid, gathered on the top of androphore, 0.5-0.6 mm long, connectives with numerous apical pustules or droplets with secretion. Pistillate flowers (fruiting) 1-2 cm diam; pedicel 1-1.2 cm long, c. 1 mm diam, villose and sparsely hispid; sepals triangular, already enlarging, c. 2 by 1 cm, finally leaf-like, persistent, margin with few teeth near top, apex acuminate, both sides hispid and often villose or ciliate along veins and margins; petals not seen, caducous; disc lobes semi-orbicular, c. 0.4 by 0.7 mm; ovary densely hispid, styles c. 0.5 mm long, stigmas completely bifid, arms c. 0.8 mm long, bent. Fruits c. 1.5 cm diam, hispid outside; wall c. 0.6 mm thick, exocarp not splitting off; columella c. 6.5 mm long. Seeds c. 6.5 mm diam, often with sparse pustules on surface; hilum elliptic, c. 4 by 2 mm, apex often apiculate.

Distribution — Malay Peninsula (endemic).

Habitat & Ecology — Primary forest to newly logged forest on hill side. Flowering: May and August; fruiting: July and September.

Note — An extremely hairy species with large accrescent pistillate sepals.

29. Trigonostemon verticillatus (Jack) Pax — Map 11

Trigonostemon verticillatus (Jack) Pax in Pax & K.Hoffm (1911) 87; Jabl. (1963) 164; Airy Shaw (1972a) 349; Whitmore (1973) 136; Chantar. (2005) 30; (2007) 585, pl. 31: 2. — Enchidium verticillatum Jack (1822) 90; (1835) 257, excl. synon. Rumphius; Müll.Arg. (1866) 1256; Merr. (1952) 224. — Neotype (designated here): Maingay KD 1403 (holo L; iso BM, K), Malay Peninsula, Malacca (see note).

Telogyne indica Baill. (1858) 328, 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 here): Wallich 7997 (G; isolecto P), Malaysia, Penang.

Small trees, up to 8 m tall; flowering branches terete, 2.5-3 mm diam. Bark 0.4-0.5 mm thick, pale greyish; wood pale yellowish. Stipules subulate, 0.5-1.5 mm long, blackish and pubescent near base, yellowish at apex. Leaves: petiole wrinkled, terete but grooved above, 2-9 cm long, often thickened at apex and base; blade oblong, sometimes elliptic or lanceolate, occasionally linear, 10-22 by (1.5-)2.5-5 cm, chartaceous or coriaceous, base acute to rounded, 1 or 2 pairs of glands adaxially present, subulate or falcate, often glabrous, margin distantly serrate, teeth subulate, apex acuminate to caudate, upper surface dark green, lower surface pale green, both sides glabrous; midrib slightly raised above and distinctly elevated beneath, nerves 12-21 pairs, connected along margin, veinlets reticulate, often obscure. Inflorescences bisexual, terminal or subterminal, racemes (spike-like) or thyrses, often puberulent, main rachis up to 10 cm long, involucral bracts triangular to lanceolate to falcate, 1–2 by c. 0.5 mm, with 2 lateral bracteoles; bracts to flowers broadly triangular, somewhat sheathing, up to 1 by 1 mm, apex acuminate, puberulent. Staminate flowers c. 4 mm diam (unopened); pedicel slightly thickened towards apex, 1.5-3 mm long, apically 0.6-0.8 mm diam, glabrous or very slightly puberulent; sepals often unequal, orbicular to ovate, 1-1.5 by 1-1.5 mm, imbricate, apex rounded, outside glabrous or slightly puberulent, margin ciliate; petals ovate, 2.5-2.8 by c. 2 mm, dark reddish, contort, apex rounded, outer surface glabrous, inner surface rough and slightly papillose, margin entire, occasionally slightly ciliate; disc annular when young and cupular when mature, c. 0.5 mm wide, margin often with 5 notches; stamens 5, androphore c. 0.5 mm long, anthers ellipsoid, c. 1 mm long, divaricate, connectives apically with numerous droplets (or expanded cells) with secretion. Pistillate flowers c. 5 mm diam; pedicel as staminate flowers but longer and thicker, c. 4 mm long, c. 1 mm diam; sepals elliptic, c. 1.5 by 1 mm when flowering, more or less accrescent to 3 by 2 mm when fruiting, apex rounded, outside slightly puberulent, margin ciliate; petals as staminate flowers, caducous; disc annular, subentire; ovary 1.2-1.5 mm diam, puberulent, style c. 0.2 mm long, sometimes indistinct, stigmas c. 0.7 mm long, bifid at apex, arms c. 0.5 mm long, thickened abaxially, reniform at base. *Fruits* c. 1 cm diam, outside finely puberulent; wall 0.7–1 mm thick, exocarp detaching. *Seeds* c. 5.5 mm diam; hilum rhombic, c. 1.8 by 1 mm.

Distribution — Vietnam, Thailand, Malay Peninsula.

Note — The genus *Enchidium*, described by Jack (1822), is reliably identical to *Trigonostemon*, even though there were a few mistakes in the manuscript, e.g., he mentioned that the plants have 10 stamens, instead of 5. The genus remained monospecific since Jack's publication. Jack's original collection from Sumatra was never checked again by later botanists and it is very likely that it does not exist anymore (Merrill 1952). The illustration Jack cited (see Rumphius 1743) is a sterile plant and does not appear to be *Trigonostemon*.

Probably on account of the obscure status of *Enchidium*, botanists tended to abandon the name even though it was validly published prior to *Trigonostemon*. For example, Hooker (1887) regarded *E. verticillatum* as synonym under the later published *T. indicus*. Jackson (1893, 1895) reduced *Enchidium* as a synonym under *Trigonostemon*. Pax & Hoffmann (1911) also transferred the type species *E. verticillatum* to *T. verticillatus* and synonymised *T. indicus* under *T. verticillatus*. The genus was eventually rejected in 1954 (see Introduction).

Because Jack's collection is not available and illustration is incorrect, a neotype is here designated to *T. verticillatus*. We followed Pax & Hoffmann's (1911) treatment and the neotype specimen is chosen from one of Pax & Hoffmann's (1911) vouchers.

Key to the varieties

- 1. Leaf blade oblong, elliptic or lanceolate, 10–22 by 2.5–5 cm. Petals with entire margin a. var. *verticillatus*
- 1. Leaf blade nearly linear, 10–16 by 1.5–2.5 cm. Petals with a slightly ciliate margin. b. var. *salicifolius*

a. var. verticillatus — Map 11

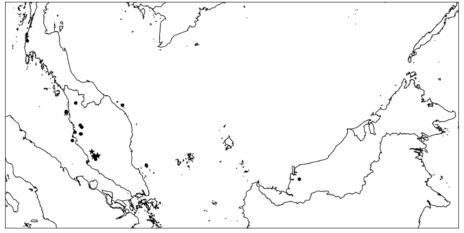
Leaves: blade oblong, elliptic or lanceolate, 10–22 by 2.5–5 cm. *Petals* with entire margin.

Distribution — Vietnam, Thailand, Malay Peninsula.

Habitat & Ecology — Primary dipterocarp forests on hillsides or near the sea, growing in peat swamps. Altitude: 60–400 m. Flowering: December to April.

b. var. salicifolius (Ridl.) Whitmore — Map 11

Trigonostemon verticillatus (Jack) Pax var. salicifolius (Ridl.) Whitmore (1972) 52; (1973) 136. — Trigonostemon salicifolius Ridl. (1923) 366; (1924) 264; Jabl. (1963) 152, f. 1; Airy Shaw (1975) 204. — Type: Ridley s.n. (holo K), Malaysia, Selangor, Kanching.



Map 11 Distribution of Trigonostemon verticillatus (Jack) Pax. var. verticillatus (♠) and T. verticillatus var. salicifolius (Ridl.) Whitmore (★).

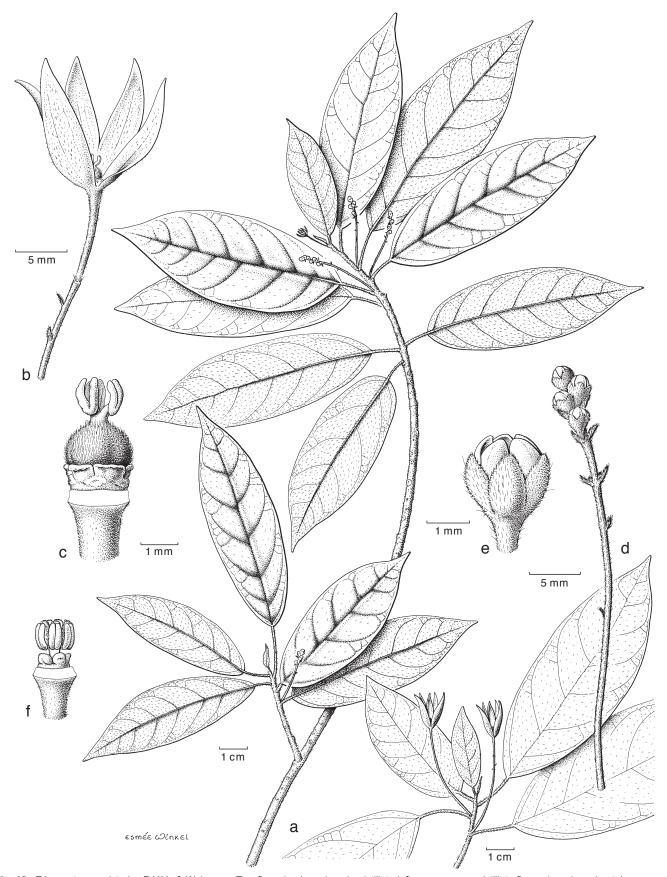


Fig. 15 *Trigonostemon victoriae* R.Y.Yu & Welzen. a. Two flowering branches; b. pistillate inflorescences; c. pistillate flower (sepals and petals removed); d. staminate inflorescence; e. staminate flower, showing the sepals and petals; f. staminate flower (sepals and petals removed) (all: *PNH* (*Sulit*) 12317, L). — Drawing by Esmée Winkel, 2016.

Leaves: blade nearly linear, 10–16 by 1.5–2.5 cm. *Petals* with a slightly ciliate margin.

Distribution — Malay Peninsula (endemic).

Habitat & Ecology — Dipterocarp forests. Altitude: 80–150 m. Flowering: January and July.

Note — This is a tentative treatment, data from a molecular phylogeny is needed. The variety mainly differs from var. *verticillatus* by having narrower leaves.

30. *Trigonostemon victoriae* R.Y.Yu & Welzen, *sp. nov.* — Fig. 15; Map 10

This species resembles *T. capillipes* in the pistillate inflorescences and enlarged pistillate sepals, but differs by having racemose staminate inflorescences, staminate flowers with 3 stamens and pistillate flowers with sepals hairy inside and glabrous ovaries. — Type: *PNH* (*Sulit*) 12317 (holo L), Philippines, Palawan Province, Victoria Mountains, Panacan, Aborlan.

Small trees, up to 6 m tall, dbh c. 10 cm; flowering branches 2-2.5 mm diam. Outer bark 0.1-0.2 mm thick, pale greyish, somewhat shiny, pubescent near apical buds and glabrescent in mature parts; inner bark 0.1-0.2 mm thick, dark reddish; wood pale yellowish. Stipules subulate, 0.5-1 mm long, often persistent, base pubescent, apex glabrous. Leaves: petiole terete but grooved above, 0.5-3 cm long, pubescent; blade elliptic, 6-11 by 2-4 cm, chartaceous to coriaceous, base acute to rounded, 2 adaxial glands present, often pubescent, margin distantly serrate, teeth glandular, apex acuminate to slightly caudate, upper side glabrous, dark red in dry specimens when young to pale grey and shiny when mature, lower side sparsely pubescent; venation penninerved, often pubescent on the lower side, especially in young leaves, midrib more or less raised above and elevated beneath, nerves 6-8 pairs, curved and narrowed along margin, veinlets reticulate. Inflorescences unisexual, racemose, staminate ones c. 5 cm long, c. 0.5 mm diam, appressed pubescent; bracts lanceolate to oblong, 1-3 by 0.3-0.6 mm, appressed pubescent; pistillate inflorescences often with only 1 flower at the top of inflorescences and sometimes a few depauperate buds below; peduncles up to 5 cm long, c. 0.5 mm diam, pubescent; bracts lanceolate to elliptic, 3–4 by 0.3–0.7 mm, pubescent. Staminate flowers (unopened) c. 3 mm diam; pedicel 0.5-1 mm long, c. 0.5 mm diam, pubescent; sepals ovate to elliptic, 1–1.5 by 0.8–1.1 mm, imbricate, margin entire, apex acute to acuminate, pubescent outside; petals orbicular, 0.9-1.1 mm diam, dark purplish, glabrous on both sides; disc lobes semi-orbicular, c. 0.2 by 0.1 mm, fleshy, apex acute; stamens 3, androphore indistinct, anthers ellipsoid, grouped at the top of androphore, c. 0.45 mm long. Pistillate flowers c. 4 mm diam; pedicel c. 3 mm long, c. 0.5 mm diam, sericeous; sepals lanceolate, 2.5-4 by 0.6-1.5 mm when flowering, accrescent to 10-13 by 2.5-4.5 mm when fruiting, margin with a few indistinct teeth, apex acute to acuminate, sericeous on both sides, denser outside; petals elliptic to ovate, 1.1-1.4 by 1-1.2 mm, glabrous except for ciliate margin; disc lobes rectangular, 0.15-0.2 by 0.2-0.25 mm, apex truncate, glabrous; ovary c. 0.65 mm diam, glabrous; styles c. 0.1 mm long, stigmas deeply divided and reniform, arms straight, c. 0.3 mm long. Fruits and seeds not seen.

Distribution — Philippines (Victoria Mountains, endemic). Habitat & Ecology — Dipterocarp forests, growing on clay, near rivers. Flowering: May.

Note — Only known from the type collection. The mature leaves often turn greyish and are shiny, but this could be a drying artefact. Another useful distinction is that *T. victoriae* only has a few small bracts along the pistillate inflorescences while its resembling species, *T. capillipes*, tends to have larger, leaf-like bracts under the pistillate flowers.

31. Trigonostemon villosus Hook.f. — Fig. 16, 17; Map 12, 13

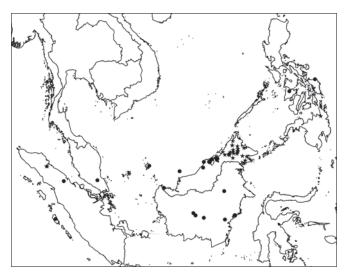
Trigonostemon villosus Hook.f. (1887) 397; Pax & K.Hoffm. (1911) 88; Ridl. (1924) 265; Jabl. (1963) 158; Whitmore (1973) 135; Airy Shaw (1975) 204; (1981) 358; R.I.Milne (1995a) 37. — Type: King's collector s.n. (holo K), Malaya, Perak.

Trigonostemon tomentellus Pax & K.Hoffm. (1911) 89. — Type: Anonymous s.n. (holo B†), Malacca.

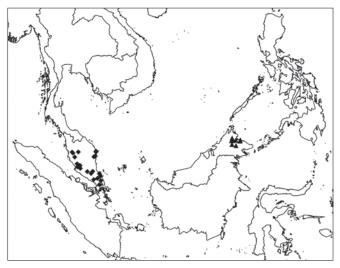
Trigonostemon carnosulus Airy Shaw (1978) 415. — Type: CF (Yeop) 844 (holo K), Malaya.

Trigonostemon polyanthus auct. non Hook.f.: R.I. Milne (1995a) 25.

Small trees, up to 6 m tall, dbh up to 6 cm; flowering branches 2.5–6 mm diam, buds pubescent. *Outer bark* 0.1–0.3 mm thick, pale brownish to greyish, often pubescent when young, glabrescent lower, sometimes fissured; inner bark 0.1–0.3 mm thick, dark reddish; sapwood 0.6–1.4 mm thick, pale yellowish; heartwood 0.6–1 mm diam, brownish, soft. *Stipules* subulate, 0.8–1.8 mm long, pubescent. *Leaves*: petiole terete but often furrowed above, 0.5–25 cm long, glabrous to hirsute, sometimes slightly thickened at base and apex; blade elliptic to oblong (Malay Peninsula, Borneo, Philippines) or oblanceolate (Sumatra), 6.5–32 by 2.5–14 cm, chartaceous, base cuneate, acute, obtuse or rarely slightly cordate (East Kalimantan), 2 adaxial glands present, margin distantly serrate, teeth small, subulate or falcate, apex acuminate to caudate,



Map 12 Distribution of *Trigonostemon villosus* Hook.f. var. *borneensis* (Merr.) Airy Shaw (★) and *T. villosus* var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen (●).



Map 13 Distribution of *Trigonostemon villosus* Hook.f. var. *villosus* (♠) and *T. villosus* var. *cordatus* R.Y.Yu & Welzen (♠).

upper side glabrous, dark green, lower side paler and to a different extent villose; midrib flat or slightly raised above and distinctly elevated beneath; nerves 7–12(–15) pairs, often bow-shaped, narrowed along margin, veins reticulate, sometimes obscure. *Inflorescences* unisexual or bisexual, racemes (pistillate ones if unisexual) or thryses, sometimes condensed, often axillary, sometimes cauliflorous, villose; rachis up to 42 cm long, 0.3–0.9 mm diam, staminate flowers clustered into short cymes or glomerules along rachis, pistillate flowers often single per node; bracts linear to lanceolate, 0.8–3.2 by

0.2–1.1 cm, margin entire (Borneo, Philippines) or serrate (Malay Peninsula, Sumatra), glabrous to villose, bracteoles (Malay Peninsula) lanceolate to linear, up to c. 5.5 by 1 mm, villose. *Staminate flowers* 3.5–6 mm diam, pedicel 2–3.5 mm long, 0.2–0.3 mm diam, pinkish (Sabah), glabrous; sepals elliptic, 2–2.5 by 1–1.4 mm, imbricate, white (Sabah), margin ciliate, apex rounded, outer surface slightly pubescent, sometimes with a very faint gland near apex, inner surface glabrous or rarely slightly villose (only one collection, *van Balgooy 2187*, Malay Peninsula); petals elliptic to obovate to spathulate, 2–3.8 by

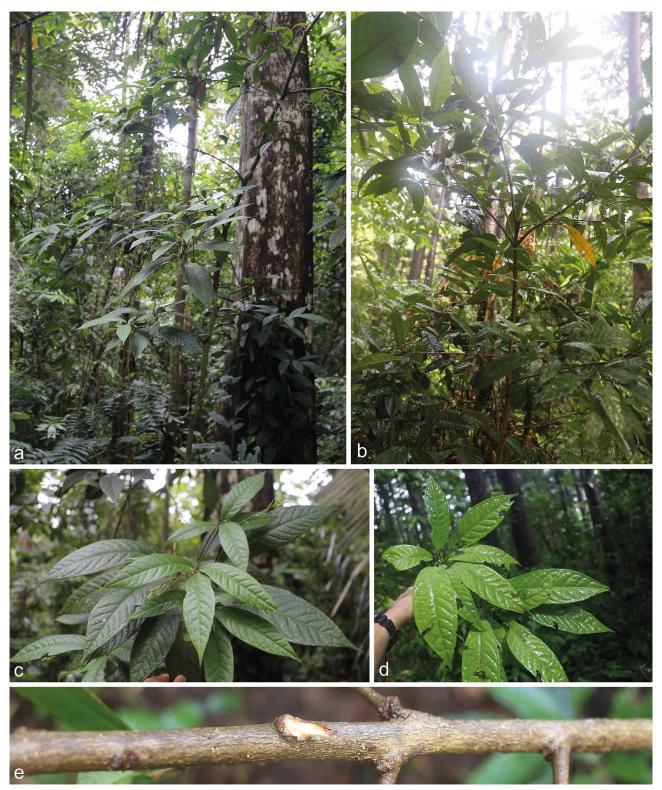


Fig. 16 *Trigonostemon villosus* Hook.f. var. *villosus* (a, c, f), Forest Research Institute Malaysia, Kepong, Malay Peninsula and *Trigonostemon villosus* Hook.f. var. *borneensis* (Merr.) Airy Shaw (b, d, e, g-m), Segaliud Lokan Forest Reserve, Sabah, Malaysia. a, b. Growing habit; c, d. top view of the tree; e. bark and reddish exude; f, g. pistillate inflorescence; h, i. staminate flower; j, k. pistillate flower; l, m. fruit. — Photos by Ren-Yong Yu.

1-2 mm, purplish black, base often with a pinkish flame-like honey mark inside (Borneo), margin entire, apex rounded, smooth and glabrous outside, rough and papillose inside; disc lobes rectangular or obtrapezoid, c. 0.5 by 0.5 mm, yellowish (Sabah), apex truncate, sometimes reflexed; stamens 3, androphore 0.4-0.9 mm long, anthers ellipsoid, 0.5-0.6 mm long, pinkish (Sabah), connectives apically with numerous reddish droplets with secretion. Pistillate flowers 6-8 mm diam, pedicel often slightly thickened towards apex, 3.5-10 mm long, apically 0.5-1.2 mm diam, green or red, glabrous to hairy; sepals lanceolate (Malay Peninsula, Sumatra) or elliptic to oblong (Borneo, Philippines), 2.5-6 by 0.8-1 mm when flowering, sometimes accrescent when fruiting, up to c. 9 by 2.3 mm, white in flowers, turning green in fruits (Sabah), margin serrate (teeth often glandular, Malay Peninsula, Sumatra) to entire (Borneo, Philippines), apex acuminate, outer surface sparsely to densely villose, sometimes with a faint abaxial gland near apex, inner surface glabrous, very occasionally villose (one collection from Malay Peninsula); petals as staminate flowers but larger and caducous, 3-5 by 1.5-2.3 mm; disc rectangular, 0.3-0.9 by 0.5-0.6 mm, membranous, apex rounded or truncate; ovary c. 1 mm diam, glabrous to densely villose, styles short, indistinct, stigmas 3, completely bifid, free arm 0.8-1.3 mm long. *Fruits* c. 0.9-1.2 cm diam, villose; wall 0.4-0.6 mm thick; columella 4-6 mm long. *Seeds* 5-6.5 by 4.5-6.5 mm, hilum heart-shaped, 1.8-3.2 by 1.4-2.4 mm.

Distribution — Malay Peninsula, Sumatra, Borneo, Philippines.

Notes — 1. Milne (1995a) misinterpreted *T. polyanthus* because he cited a wrong type specimen. The actual *T. polyanthus* is a very distinct species, differing from *T. villosus* in its penicillate or fastigiate inflorescences.

2. This species consists of four varieties spreading over a huge area (Map 12, 13) of great morphological variation. We made this treatment based on a large number of collections showing that this massive variation actually connects all single



Fig. 16 (cont.)

forms together into a species complex, even though the extreme forms often do not resemble each other (see Fig. 18). These extremes, furthermore, have often become the source of synonyms, where the species status is only valid in the type locality, but in a larger area, intermediate forms are always found. As morphological discontinuities are the only valid argument for species / variety delimitation, all the forms in Fig. 18 are regarded as a single species despite the wide distribution; and *T. villosus* var. *cordatus* is described as a separate variety, regardless of its small distribution area (Sabah).

3. Generally, the hairs on leaf surfaces, the size of petioles and leaf blades and the inflorescence structure can be good characters to tell the varieties apart.

The varieties *villosus* and *borneensis* all have relatively stable and similar leaf blade and petiole sizes (Fig. 16), but they

are different in inflorescence and flower structures – in var. borneensis, the inflorescences are unisexual (vs bisexual in var. villosus, but staminate flowers often fall off), the pistillate inflorescences have fewer flowers (often fewer than 4) at a time (vs often more than 4 in var. villosus), and the pistillate sepals are not much accrescent and often have an subapical gland outside (vs obviously accrescent and with a faint or no gland in var. villosus).

The new variety *cordatus* has a hairy leaf blade, which forms a typical morphological discontinuity separating it from var. *borneensis*.

The variety *merrillianus* is different from var. *borneensis* by its much (variable) longer petioles, much larger blades, often leaf-like bracts and staminate flowers in condensed glomerules.



Fig. 17 Trigonostemon villosus Hook.f. var. cordatus R.Y.Yu & Welzen, from Kabili-Sepilok Forest Reserve (a, e, f) and Tawai Forest Reserve (b-d, g), Sabah, Malaysia. a. Growing habit; b. juvenile tree, showing the leaves; c. bark and wood; d. staminate inflorescence; e. staminate flower; f. pistillate flower; g. fruit. — Photos by Ren-Yong Yu.

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var. villosus

T. carnosulus; T. tomentellus

Malaya: King's collector s.n., FRI (P. Vethevelu 29673), R.Y. Yu 173, 178: petiole 3–8 cm; blade 12–18 by 3.5-5.5 cm, glabrous to villose above; infl. bisexual, fl. ♀ single per node, fl. ♂ a cyme per node; sepals ♂ gland 0 or faint, ♀ serrate; ovary densely villose.

infl.: bisexual → unisexual; fl. ♂ often cauliflorous;

leaves cordate at base infl.: bisexual → unisexual; fl. ♂ often cauliflorous;

fl. ♀ 1 present at a time;

var. **cordatus**

Sabah and E Kalimantan: SAN (R.Y.Yu & Jemson) 118479: petiole 0.5-2.5 cm; blade 8.5-22 by 3.5-9.5 cm; infl. unisexual, ♂ thyrses, a cyme per node, ♀ racemes; sepals ♂ gland 0, ♀ entire; ovary glabrous to densely villose.

> blade (upper surface): glabrous → pubescent;

Sabah and Philippines: Elmer 20472, SAN (M.Chai) 31638, SAN (R.Y.Yu et al.) 158452, Wenzel 186: petiole 0.5-5.5 cm; blade 5.5–18 by 2.5–6.5 cm, glabrous above: infl. unisexual. 3 thyrses, a cyme per node, ♀ racemes; sepals ♂ gland showy, sepals ♀, entire, ovary villose.

var. **borneensis**

T. wenzelii:

T. borneensis;

T. hirsutus

petiole shorter; fl. \supseteq 1 at top of infl. Sumatra: W.J.J.O de Wilde & B.E.E de Wilde-Duvfies 19367, 21244. 21362: petiole 0.5-2.5 cm; blade 7–18 by 3–6.5 cm. glabrous above: infl. unisexual. thyrses. fl. 2 1–2 at top, fl. 3 a cyme per node; sepals ♂ gland 0, ♀ serrate; ovary densely villose

blade larger; petiole longer; infl. often with large bracts

fl. $\[\land \]$ more condensed: cymes $\[\rightarrow \]$ glomerules;

Philippines: BS (Ramos) 24528, PNH (M.D.Sulit) 14361; petiole 2.5-7.5 cm, blade 14-23 by 3.5-6 cm, glabrous above; infl. unisexual, ♂ thyrses, a cyme or glomerule per node, ♀ racemes; sepals ♂ gland obsure, ♀ entire; ovary villose.

> petiole longer, blade larger; infl. & highly condensed; ovary becomes glabrous

Sarawak and Brunei: Hose 420, S (P.S. Ashton) 18103, S (S.ak Luang) 26123, S (E. Wright) 29123, K.M. Wong 1293: petiole 3-25 cm; blade 20-32 by 4.5-14 cm, glabrous both sides; infl. unisexual, ♂ thyrses, a dense glomerule per node, ♀ racemes; sepals ♂ gland showy, ♀ entire; ovary glabrous.

petiole longer; blade larger; ovary less hairy

04-25, C. Bernard 9757, s.n.: petiole 0.5-10 cm; blade 8–30 by 2.5–14 cm, glabrous above; infl. unisexual, ♂ thyrses, a cyme or glomerule per node, ♀ racemes; sepals ♂ gland obscure, ♀ entire or crenate; ovary glabrous to slightly hairy.

E Kalimantan: Ambriansyah AA220, F. Slik

var. merrillianus

T. acuminatus; T. laxiflorus;

T. merrillianus

petiole becomes longest; blade becomes largest; infl. ♂ highly condensed

petiole longer; ovary totally glabrous

W Kalimantan: Veldkamp 8582: petiole 7-10 cm; blade 20-25 by 8-10 cm, glabrous above; infl. unisexual, ♂ thyrses, a cyme or glomerule per node, ♀ racemes; sepals ♂ gland obscure, ♀ serrate; ovary glabrous.

Fig. 18 Continuous morphological variation of T. villosus. Frames in dashed lines refer to the varieties, the accepted name of each variety is in bold with synonyms shown below it; frames in solid lines refer to intermediate forms among the variation with example specimens; arrows between the frames indicate how a variety / form continuously varies into another (the arrows are one-sided to describe transitions, but these transitions may also have happened in the other direction). Abbreviations: fl. = flowers, infl. = inflorescences. The type collection of each variety is shown in bolditalic.

Key to the varieties

1. Petiole longer than 8 cm d. var. <i>merrillianus</i>
1. Petiole shorter than 8 cm
2. Inflorescences bisexual. — Malay Peninsula
a. var. <i>villosus</i>
2. Inflorescences unisexual
3. Leaves glabrous above. — Sumatra, Sabah, Philippines)
b. var. borneensis
3. Leaves pubescent above. — Sabah c. var. cordatus

a. var. villosus — Fig. 16; Map 13

Leaves: petiole 3–8 cm long; blade oblong, 12–18 by 3.5–5.5 cm, glabrous to glabrescent (rarely villose) above and villose beneath. *Inflorescences* bisexual or unisexual (often because staminate flowers fallen), thyrsoid, 6–16 cm long, one pistillate flower and a few staminate flowers per node, often more than 4 pistillate flowers present at one time. *Staminate flowers*: sepals often without a subapical gland; petals elliptic, honey mark unseen. *Pistillate flowers*: sepals lanceolate, apex acuminate, margin often serrate, always accrescent when fruiting; ovary villose. *Fruits* villose.

Distribution — Malay Peninsula (endemic).

Habitat & Ecology — Understorey in primary forests to logged-over areas, often on hill sides or along rivers, growing in swamps forests, on peaty soil. Flowering: January, May, June, October, November; fruiting: January, April to June, October, November.

b. var. borneensis (Merr.) Airy Shaw — Fig. 16; Map 12

Trigonostemon villosus Hook.f. var. borneensis (Merr.) Airy Shaw (1975) 205. — Trigonostemon borneensis Merr. (1929) 162; Jabl. (1963) 162; Whitmore (1973) 136. — Type: Elmer 20742 (holo PNH†; iso A, BISH*, BM, BR*, CAS*, CM*, G*, GH*, HBG*, K, L, M*, MICH*, NY*, P*, PH*, S*, SING, U, UC*), Borneo, near Tawao.

Trigonostemon hirsutus C.B.Rob. (1911) 335; Pax & K.Hoffm. (1914) 406; Merr. (1923) 451; Airy Shaw (1983b) 47; R.I.Milne (1995a) 28, in key, 30, in key, 41, f. 3. — Type: BS (Robinson) 11798 (holo PNH†, not seen), Philippines, Mindanao, Zamboanga District, Port Banga (synonymy somewhat doubtful as the type is lost).

Trigonostemon wenzelii Merr. (1913) 380; Pax & K.Hoffm. (1919) 41; Merr. (1923) 453. — Type: Wenzel 186 (holo PNH†; iso A*, G*, GH*, L, US*), Philippines, Leyte, Dagami.

Trigonostemon villosus Hook.f. var. caesius R.I.Milne (1995a) 28, in key, 30, in key, 37. — Type: SAN (Ampuria) 40236 (holo K; iso SAN), Sabah, Beaufort District, Beaufort Hill.

Leaves: petioles 0.5–5.5 cm long; blade elliptic to obovate, 5.5–18 by 2.5–6.5 cm, glabrous above, often pubescent beneath. *Inflorescences* unisexual, up to 16 cm long, staminate ones racemose or thyrsoid, sometimes cauliflorous, a few flowers per node, never clustered as glomerules; pistillate ones racemose, often fewer than 4 flowers present at one time. *Staminate flowers*: sepals pink, often with a showy gland near the apex outside; petals obovate, with an orange to yellowish flame-like honey mark near the base. *Pistillate flowers*: sepals elliptic, margin entire; ovary villose. *Fruits* green when young, red when mature, glabrous to pubescent.

Distribution — Sumatra, Borneo (Sabah), Philippines.

Habitat & Ecology — Primary lowland rainforests, often on hillsides or near rivers, growing on well-drained brown loam soil. Flowering: June to December; fruiting: July to December.

Note — Some collections from Sumatra (e.g., *W.J.J.O de Wilde & B.E.E de Wilde-Duyfjes 19367, 21244, 21362*) display an intermediate form between the variety *villosus* and variety *borneensis*. They have short petioles (shorter than 2.5 cm), seemingly unisexual inflorescences and often 1 or 2 pistillate flowers per inflorescence at one time, which all show clear al-

legiance to var. *borneensis*. Because of this, they are tentatively placed under var. *borneensis* even though there is a huge gap between their main distribution locations (Sumatra, Sabah), but the serrate sepals of the pistillate flowers with an acuminate apex do somewhat resemble var. *villosus*.

c. var. cordatus R.Y.Yu & Welzen, var. nov. — Fig. 17; Map 13

A variety found in Sabah resembling *Trigonostemon villosus* Hook.f. var. borneensis (Merr.) Airy Shaw but differs from the latter by the leaves often being cordate at base and pubescent on the upper surface. — Type: *SAN (R.Y.Yu & Jemson) 158479* (holo L; iso SAN), Sabah, Sandakan, Kabili-Sepilok Forest Reserve. Paratypes: *SAN (R.Y.Yu et al.) 158458* (L, SAN), Sabah, Tepid, Tawai Forest Reserve; *SAN (R.Y.Yu et al.) 158459* (L, SAN), Sabah, Tepid, Tawai Forest Reserve; *SAN (R.Y.Yu et al.) 158460* (L, SAN), Sabah, Tepid, Tawai Forest Reserve; *SAN (R.Y.Yu & Jemson) 158480* (L, SAN), Sabah, Sandakan, Kabili-Sepilok Forest Reserve; *SAN (R.Y.Yu & Jemson) 158481* (L, SAN), Sabah, Sandakan, Kabili-Sepilok Forest Reserve; *Stone 6747* (KLU, L), Sabah, Sandakan, Kabili-Sepilok Forest Reserve; *SAN (Asik Mantor) 113362* (SAN), Sabah, Ulu Sg. Mantuluk Witti Range area.

Leaves: petiole 0.5–2.5 cm long; blade elliptic, 8.5–22 by 3.5–9.5 cm, often cordate at base, pubescent on both sides. Inflorescences unisexual, racemose or thyrsoid, 6–14 cm long, staminate flowers often cauliflorous, a few flowers per node along the rachis. Staminate flowers: sepals elliptic, white; petals claw-like, with a flame-like honey mark near the base. Pistillate flowers: sepals elliptic, green, apex rounded, margin entire, slightly accrescent in fruit; ovary glabrous to densely villose. Fruits green, pubescent.

Distribution — Borneo (Sabah, endemic).

Habitat & Ecology — Lowland rainforests, often on ultramafic soil. Flowering: December to March; fruiting: December.

Note — This variety is sometimes misidentified as *T. merrillii* because of the hairy leave surfaces, but from its racemose or thyrsoid inflorescences (very few flowers per node, certainly not short paintbrush-like glomerules as in *T. merrillii*) it easily differs from the latter species.

d. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen, *comb. nov.* & *stat. nov.* — Map 12

Trigonostemon merrillianus Airy Shaw (1971) 549, non *T. borneënsis* Merr.; (1975) 203. — *Dimorphocalyx* (?) *borneënsis* Merr. (1916a) 73. — Type: Hose 420 (holo K; iso L), Sarawak, 4th Division, Baram District, Entoyut River.

Trigonostemon acuminatus Merr. (1916b) 190; Pax & K.Hoffm. (1919) 41; Merr. (1923) 451; Airy Shaw (1983b) 46. — Type: BS (Ramos) 24528 (holo PNH†; iso A, BM, BO, K, L, US), Philippines, Samar, Catubig River. Trigonostemon laxiflorus Merr. (1920) 567; (1923) 451; Airy Shaw (1983b) 47. — Type: BS (Ramos & Edaño) 31097 (holo PNH†; iso A*, K, P*, US*), Philippines.

Leaves: petioles 1–25 cm long; blade ovate to elliptic, 8–32 by 2.5–14 cm, both sides often glabrous. Inflorescences unisexual, barely branched thyrses, up to 42 cm long, often with one large and leaf-like bract under each branch; staminate flowers often cauliflorous or in densely clustered glomerulus (Borneo) or cymes (Philippines) along a robust rachis; pistillate inflorescences racemose, robust and erect. Staminate flowers: sepals often with a faint to showy gland near the apex outside; petals sometimes with an orange to yellowish flame-like honey mark inside near the base. Pistillate flowers: sepals elliptic, entire to serrate, when serrate then teeth glandular; ovary often glabrous, occasionally slightly pubescent. Fruits pubescent.

Distribution — Borneo, Philippines.

Habitat & Ecology — Understorey in primary to burned or logged-over forests, sometimes on hill tops or slopes or along riversides, growing on red clay loam soil. Altitude: 50–900 m. Flowering: February to June, October to December; fruiting: September to May.

Note — This variety has the most variable petioles and leaf blades and more condensed staminate flowers on inflorescences: the plants from the Philippines have relatively shorter petioles, smaller blades and less condensed staminate flowers on each inflorescence node, whereas the plants from East and West Kalimantan have longer petioles (up to 25 cm long) and larger blades; in Sarawak (type locality) and Brunei, the plants have the most condensed glomerules along the staminate inflorescences. For more details, see Fig. 18. In fact, this massive variation was also seen by Milne (1995a) when he tried to synonymise *T. acuminatus*, *T. borneensis* and *T. merrillianus* under *T. polyanthus*, although *T. villosus* (not *T. polyanthus*) is the correct species name.

32. Trigonostemon viridissimus (Kurz) Airy Shaw — Map 14

Trigonostemon viridissimus (Kurz) Airy Shaw (1971) 545; Whitmore (1973) 135; Airy Shaw (1975) 205; (1981) 358; (1982) 36; (1983b) 48; R.I.Milne (1995a) 28, in key, 29, in key. — Sabia viridissima Kurz (1872) 304; Hook.f. (1876) 3; Kurz (1877a) 301. — Blachia viridissima (Kurz) King (1896) 455, in obs. — Kurziodendron viridissimum (Kurz) N.P.Balakr. (1966) 68, pl. 1, f. 1–7. — Type: Kurz s.n. (K, barcodes K000246871, K000246872), India, Andamans.

Trigonostemon ovatifolius J.J.Sm. (1910) 583; Backer & Bakh.f. (1963) 495.

— Type: Koorders s.n. (BO?, not seen), Java.

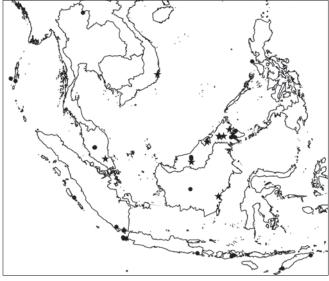
Trigonostemon membranaceus Pax & K.Hoffm. (1911) 91. — Type: Koorders 32989 (BO), Java: Djapara.

Trigonostemon sumatranus Pax & K.Hoffm. (1911) 90; S.Moore (1925) 100 (as synonym of *T. forbesii* Pax = Wetria insignis (Steud.) Airy Shaw); Merr. (1935) 101; Jabl. (1963) 163 (see note under *T. philippinensis*); W.L.Stern (1967) 671; Whitmore (1973) 135. — Type: Forbes 2647 (BM, K, L), Sumatra.

Trigonostemon macgregorii Merr. (1920) 566; (1923) 452. — Type: *BS* (*McGregor*) 32424 (holo PNH†; iso K, P, US), Philippines, Panay, Antique Province, Culasi.

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

Shrubs or small trees, up to 9 m tall, stem up to 10 cm diam; flowering branches 1.5–3 mm diam, sometimes hollow. *Bark* c. 0.3 mm thick, young parts pale and pubescent, sometimes with numerous oil-like spots, mature parts dark, brownish to greyish, glabrescent; wood pale yellowish. *Stipules* subulate to nipple-like, c. 0.5 mm long, caducous, often pubescent. *Leaves*: petiole terete but grooved above, 0.5–1.5(–5.5) cm long, wrinkled, pubescent; blade ovate to elliptic to oblong, sometimes lanceolate, 8–24 by 2.5–9 cm, membranous or chartaceous, often with numerous oil-like spots when young,



Map 14 Distribution of *Trigonostemon viridissimus* (Kurz) Airy Shaw var. *viridissimus* (\bullet) and *T. viridissimus* var. *elegantissimus* (Airy Shaw) Airy Shaw (\star).

base acute or obtuse, often with 1 or 2 pairs of adaxial glands, margin entire or slightly distantly serrate, apex acuminate to caudate, upper side glabrescent to glabrous, dark green, lower side often sparsely pubescent, paler and dull green; venations triplinerved, midrib and 2 basal nerves slightly raised above and well elevated beneath, often pubescent, especially near base, other nerves 6-10 pairs, bow-shaped and connected along margin, veins scalariform, veinlets reticulate. Inflorescences bisexual (but mostly unisexual), often axillary, loose paniculate, often with oil-like spots on young parts; main rachis terete, up to 25 cm long, c. 2 mm diam, slightly pubescent; branches slender and glabrescent; bracts lanceolate, up to 2 mm long, pubescent. Staminate flowers 5-9 mm diam; pedicel up to 9 mm long, c. 0.2 mm diam, glabrescent or slightly pubescent, often with numerous oil-like spots; sepals elliptic or orbicular, 1–1.5 by 0.6–1.2 mm, imbricate, margin somewhat undulate, apex rounded or truncate, often with a short notch, outer surface pubescent, often with numerous oil-like spots and a gland in the middle; petals obovate, 4-6.5(-10) by 3.5-4.5(-7) mm, contort, membranous, with several distinct parallel veins, base cuneate or somewhat claw-like, apex rounded, glabrous; disc annular, margin undulate, reflexed, sometimes with 5 notches; stamens 3, androphore 0.7-1.5 mm long, filaments 0.3-0.4(-0.6) mm long, anthers free, ellipsoid, 0.4-0.5 mm long. Pistillate flowers 5-9 mm diam, pedicel slightly thickened towards apex, 1-1.4 cm long, apically c. 0.5 mm diam when flowering, elongating up to 3 cm long and c. 1.4 mm diam in fruit, glabrescent, often with oil-like spots; sepals, petals and disc as staminate flowers, except petals caducous when fruiting; ovary 0.8-1 mm diam, glabrous, with numerous oil-like spots on surface, styles 0.2-0.6 mm long, stigmas 0.6-1.5 mm long, bent, slightly thickened and slightly bifid at apex. Fruits c. 1.5 cm diam, greenish, glabrous and with numerous oil-like spots, sepals persistent but not accrescent; wall c. 0.5 mm thick, exocarp detaching; columella c. 5 mm long. Seeds 7-8 mm diam, with numerous oil-like spots on surface; hilum rhombic, c. 1.5 by 1.2 mm.

Distribution — China, India, Thailand, Laos, Vietnam, Malay Peninsula, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands

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

Note — In addition to the Malesian region, this species is also found in China, India, Thailand, Laos and Vietnam under different names, all synonyms except *viridissimus*, which is the oldest and accepted epithet for this species.

Key to the varieties

- 1. Petioles often shorter than 1.5 cm, pubescent. Inflorescences axillary, pendulous, often pubescent . . a. var. *viridissimus*
- 1. Petioles longer than 1.5 cm, glabrous. Inflorescences terminal or subterminal, erect, glabrous b. var. *elegantissimus*

a. var. viridissimus — Map 14

Leaves: petiole 0.5–1.5(–5) cm long, pubescent; blade elliptic to ovate, glabrescent above, pubescent beneath. *Inflorescences* often axillary, pendulous, often pubescent.

Distribution — Malay Peninsula, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands.

Habitat & Ecology — Growing on reddish clay soil. Altitude: 0–450 m. Flowering: all year round; fruiting: January, May, July, November.

Note — A widely distributed variety with obvious triplinerved venation, paniculate inflorescences with few branches, free anthers (free parts of filaments often more than 0.3 mm long), glabrous ovary and often oil-like spots on the flowers and fruits.

b. var. elegantissimus (Airy Shaw) Airy Shaw — Map 14

Trigonostemon viridissimus (Kurz) Airy Shaw var. elegantissimus (Airy Shaw) Airy Shaw (1975) 206. — Trigonostemon elegantissimus Airy Shaw (1966) 48; (1978) 417; Whitmore (1973) 135; R.I.Milne (1995a) 28, in key, 29, in key, 47. — Type: Kostermans 13695 (holo K; iso A*, BO, K, L), E Kalimantan, Sangkulirang District, Karangan River, near Batu Pondong. Trigonostemon sanguineus Gagnep. (1925a) 470. — Type: Poilane 8201 (K,

P), Vietnam, km 26 route from Nhatrang to Ninh Hoa.

Leaves: petiole 1.5–5.5 cm long, glabrous to slightly pubescent; blade oblong to lanceolate, glabrous above, glabrous to sparsely pubescent beneath. *Inflorescences* often terminal or subterminal, erect and firm, glabrous.

Distribution — Vietnam, Malay Peninsula, Borneo.

Habitat & Ecology — Growing on sandy loam to sandy stone. Altitude: 170–230 m. Flowering: March to September; fruiting: July, October.

Note — The form *elegantissimus* is here recognized as a variety, following Airy Shaw (1975). The two varieties closely resemble each other in their floral structures, like the contort petals, the slender long and only shortly bifid stigmas. The length of the petiole and the shape of the leaf blade also show some overlap. Milne (1995a) presents a good discussion on the differences between the two varieties although he treated them as two separate species.

Trigonostemon wetriifolius Airy Shaw & Ng — Fig. 19; Map 10

Trigonostemon wetriifolius Airy Shaw & Ng (1978) 237. — Type: *KEP FRI (F.S.P. Ng)* 27157 (holo K; iso KEP), Malaysia, S Pahang, Lesong Forest Reserve in proposed Endau-Rompin National Park.

Small trees, 3 m tall, stem single, erect, 10–12 mm thick; flowering branches up to 1.2 cm diam, adventitious roots present, 0.5–1 mm thick, puberulent. *Bark* c. 0.6 mm thick, brownish to greyish, smooth to fissured; sapwood c. 2 mm thick, yellowish; heartwood 3–4 mm diam, whitish. *Stipules* subulate, 3–4 by c. 1 mm, apex acute, puberulent, caducous. *Leaves* clustered on the top of the stem; petiole c. 1.8 cm long, c. 5 mm diam,

slightly pubescent; blade spathulate to oblanceolate, 35-62 by 9–19 cm, chartaceous, base rounded, adaxial glands not seen, margin distantly serrate, apex acuminate, both sides glabrous; venation penninerved, slightly pubescent on lower side, midrib robust, slightly raised on both sides, nerves 27-30 pairs, curved, veins scalariform, veinlets reticulate. Inflorescences axillary, 1-3 cm long, few-flowered, 1 pistillate flower at top and a few staminate flowers below, rachis appressed puberulent; bracts subulate, 1–5 mm long, puberulent. Staminate flowers c. 4 mm diam; pedicel 1–2 mm long, glabrous; sepals rounded to ovate, 2-3 by 1-2 mm, apex obtuse, pubescent outside, inside glabrous; petals ovate, 1-1.5 by 1-1.5 mm, fleshy, glabrous, yellowish except reddish at base, apex obtuse; disc lobes more or less square, fleshy, c. 0.3 by 0.5 mm; stamens 5, androphore short, hidden, anthers ellipsoid, c. 0.5 mm long, divaricate at apex. Pistillate flowers (unopened): pedicel, sepals, petals and disc as staminate flowers; ovary glabrous; styles short, stigmas slightly bifid. Fruits and seeds unknown.

Distribution — Malay Peninsula (Lesong Forest Reserve, endemic).

Habitat & Ecology — Primary lowland forest under logging. Flowering: September.

Note — Only known from the type specimen. Two slides of the plant (see Fig. 19, taken by Francis Ng) are attached with the type specimen. Descriptions of staminate flowers are mainly based on the slides, thus the measurements might not be exactly accurate, since a scale was unavailable; other parts of descriptions are based on Airy Shaw & Ng (1978). The species resembles *T. detritiferus* in morphology and living strategy, for more details, see notes under *T. detritiferus*.

34. *Trigonostemon wildeorum* R.Y.Yu & Welzen, *sp. nov.* — Fig. 20; Map 10

This species resembles *T. aurantiacus*, but differs in the flowers with the sepals covered by dense silky hairs and in the 5 (in stead of 3) stamens. — Type: *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 20274* (holo L; iso BO), Indonesia, North Sumatra, Atjeh, Middle Alas River (Lae Sauraya) area, c. 15 km N of Gelombang, S of Bengkong River, N2°55' E99°57'. Paratype: *W.J.J.O*





Fig. 19 *Trigonostemon wetriifolius* Airy Shaw & Ng, Lesong Forest Reserve, Malay Peninsula. a. Growing habit, leaves arranged in whorls at top of main stem and trap fallen leaves; b. cauliflorous staminate flower. — Used with permission from Francis Ng.

de Wilde & B.E.E de Wilde-Duyfjes 18742 (BO, KLU, L, P), Indonesia, North Sumatra, Atjeh, southern part of the reserves, Alas River valley, near the mouth of the Bengkong River, c. 50 km S. of Kutacane, N3° E97°50'.

Small trees, 2–4.5 m tall; flowering branches 1.5–3 mm diam, buds golden sericeous. *Bark* c. 0.3 mm thick, pale greyish, appressed sericeous to hirsutulous when young, often smooth and fissured when mature; sapwood c. 2 mm thick, brownish; heartwood c. 2 mm diam, whitish. *Stipules* subulate, 0.5–0.6 mm long. *Leaves*: petiole terete, 0.5–1 cm long, flat above, rounded beneath, appressed hirsutulous; blade obovate, 7.5–22 by 3.5–7.5 cm, chartaceous to coriaceous, base cuneate to acute, 2 adaxial glands present, these subulate to falcate, caducous, margin entire to distantly serrate, ciliate, teeth small and falcate, apex caudate, tip 0.8–2.5 cm long, sometimes slightly slanting, upper side dark brownish (when dry), sparsely sericeous when young, pale brownish to greyish (when dry), glabrescent when mature, lower side brownish, sparsely seri-

ceous; venation penninerved, midrib flat above and elevated beneath, hirsutulous to sericeous on both sides, nerves 8-12 pairs, straight, branched and slightly curved along margin, often hirsutulous beneath, veinlets reticulate. Inflorescences reduced to a cauliflorous fascicle of at most 3 flowers; bracts oblong to linear, 1-2.5 by 0.3-0.5 mm, hirsutulous. Staminate flowers c. 6 mm diam; pedicel c. 0.5 mm long, 0.3-0.4 mm diam, densely hirsutulous; sepals elliptic, 1.5-2 by 0.8-1.3 mm, base connate, margin entire, apex acute to rounded, outside densely sericeous to hirsutulous, inside slightly floccose; petals obovate, c. 3.5 by 2.5 mm, dark purplish black, base slightly claw-like, entire, apex rounded, glabrous on both sides, few dark palmate veins often visible; disc lobes semi-orbicular, 0.4-0.5 by 0.6–0.8 mm, apex sometimes with a shallow notch; stamens 5, monadelphous, androphore erect, c. 1 cm long, c. 0.3 mm diam, anthers free, ellipsoid, divaricate, each theca c. 0.5 by 0.3 mm. Pistillate flowers c. 5 mm diam (not fully opened); pedicel

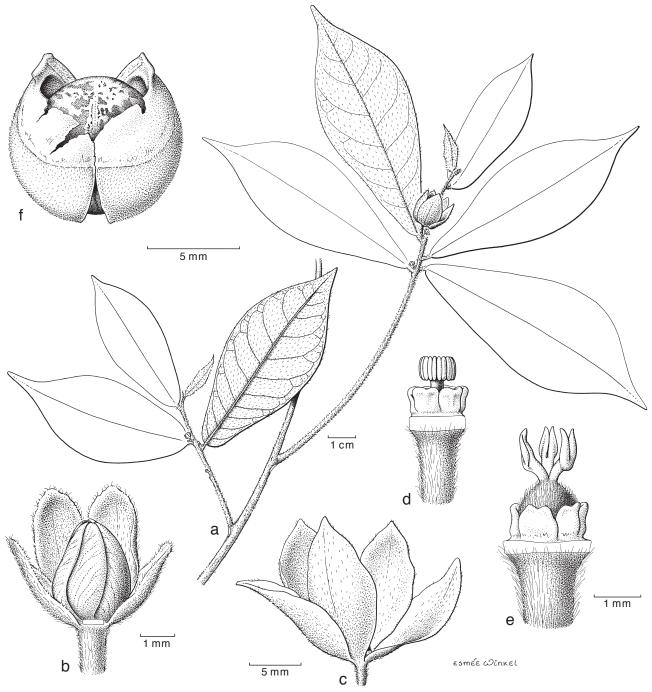


Fig. 20 *Trigonostemon wildeorum* R.Y.Yu & Welzen. a. Flowering branch; b. staminate flower, showing the sepals and petals (one sepal removed); c. pistillate flower, showing the accrescent sepals; d. staminate flower (sepals and petals removed); e. pistillate flower; f. one dehiscing coccus with a marbled seed (all: *W.J.J.O de Wilde* & *B.E.E. de Wilde-Duyfjes* 20274, L). — Drawing by Esmée Winkel, 2016.

c. 1 mm long, apically c. 1 mm diam, slightly thickened near apex, densely pubescent; sepals triangular, 3-3.5 by 1.5-2.5 mm, base narrowed and connate, margin serrate, apex acuminate, outside densely hirsutulous to sericeous, inside hirsutulous to pubescent, accrescent in fruits, then elliptic to ovate, up to 1.3 by 1 cm, base rounded to truncate, margin distantly serrate, apex acute, sometimes with a small notch, outside a few palmate veins visible, sericeous especially on veins, inside sparsely sericeous; petals ovate to elliptic, c. 2.5 by 1.5-2 mm, dark purplish black, caducous, margin entire, apex acute to acuminate, glabrous; disc lobes as staminate flowers; ovary c. 0.8 mm diam, densely pubescent, style indistinct, stigmas c. 0.9 mm long, deeply bifid, arms c. 0.7 mm long, thickened and slightly sagittate at base. Fruits c. 1 cm diam, puberulent outside; wall c. 0.5 mm thick, exocarp partly splitting off; columella c. 5 mm long. Seeds c. 6 mm diam.

Distribution — Sumatra (endemic).

Habitat & Ecology — Primary foothill forest on yellow-red loamy soil over basalt rock. Altitude: 50–200 m. Flowering and fruiting: July.

Note — Only known from the two collections mentioned above.

DOUBTFUL SPECIES

35. Trigonostemon angustifolius Merr. — Map 15

Trigonostemon angustifolius Merr. (1922) 396. — Type: BS (Ramos & Edaño) 36764 (of 36560) (holo PNH†; iso A, K, US), Philippines, Mindanao, Zamboanga District, Malangas.

Shrubs, 1-3 m tall; flowering branches c. 3 mm diam. Outer bark c. 0.1 mm thick, white to grey, smooth, slightly pubescent when young, glabrescent; inner bark 0.2-0.3 mm thick, dark brownish; wood white to yellow. Stipules very small, pointing, appressed pubescent, caducous. Leaves: petiole terete but grooved above, 5-8 mm long, 1.2-1.5 mm diam, appressed pubescent; blade oblong, 10-15 by 2-3 cm, chartaceous, base acute, glands not seen, margin distantly serrate, teeth glandular, apex acuminate to shortly caudate, upper surface dark brown to black (when dry), glabrous, lower surface reddish brown, slightly pubescent; midrib slightly raised and glabrous above, distinctly elevated and pubescent beneath, nerves 8-11 pairs, pubescent beneath, veins reticulate, obscure above. Inflorescences: staminate ones not seen; pistillate ones axillary, slender, peduncled, a glomerule at apex; peduncle c. 5 cm long, c. 0.5 mm diam, appressed pubescent; glomerules few-flowered, subtended by two bracts (also one bract present on the lower node), bracts lanceolate, 10–12 by 2–3 mm, appressed pubescent beneath. Staminate flowers not seen. Pistillate flowers: sepals lanceolate, c. 6 by 2.5 mm, apex acuminate, outside eglandular, slightly pubescent; petals 5–6 mm long, glabrous, dark purple; ovary glabrous, styles 3, stigmas cleft nearly to the base, arms linear, 1.5 mm long, acuminate. Fruits depressed globose, c. 12 mm diam, brown, sparingly appressed pubescent, sepals accrescent up to 12 by 6 mm. Seeds not seen.

Distribution — Philippines (Mindanao, endemic).

Habitat & Ecology — On forested slopes at low altitudes (Merrill 1922). Flowering: October.

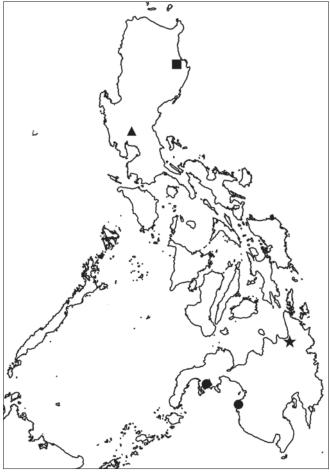
Vernacular name — Pululi (Merrill 1922).

Note — The species is only known from the type collection. Due to the insufficient material seen the descriptions of pistillate flowers and fruits are based on Merrill (1922). Knowledge on the staminate flowers of the species is still lacking and, therefore, it is impossible to even determine whether the species belongs to *Trigonostemon* or not.

36. Trigonostemon cumingii Müll.Arg. — Map 15

Trigonostemon cumingii Müll.Arg. (1865) 213; (1866) 1107. — Tritaxis cumingii (Müll.Arg.) Benth. (1878) 221; Pax (1910) 114; Merr. (1923) 449. — Dimorphocalyx cumingii (Müll.Arg.) Airy Shaw (1969) 124; (1983b) 20. — Type: Cuming 1693 (holo P*; iso BM, E*, G*, K, L, P*), Philippines, Samar.

Shrubs, 0.3–0.5 m tall, dbh up to 4 cm; flowering branches 1–2.9 mm diam. Outer bark c. 0.1 mm thick, black to brown, smooth, puberulent when young, glabrescent; inner bark 0.1-0.2 mm thick, dark reddish; wood white to yellow. Stipules elliptic, 1.5-2 by 0.5-1 mm, appressed pubescent, caducous. *Leaves*: petiole terete but grooved above, 0.8-4.5 mm long, 0.9-1.1 mm diam, often more or less appressed pubescent; blade elliptic, 9-16 by 4-7.5 cm, coriaceous to chartaceous, base acute to rounded, without glands, margin crenate, teeth glandular, apex acuminate to shortly caudate, upper surface brown to black (when dry), lower surface pale brown, both sides pubescent when young, glabrous when mature; midrib flat above, elevated beneath, nerves 7-9 pairs, veins reticulate, obscure above. Inflorescences: staminate ones axillary, peduncled; peduncles sometimes short and with few branches, 0.5-1.7 cm long, 1–1.5 mm diam, appressed pubescent; bracts elliptic, 1.5–3 by 0.5-1.2 mm, margin slightly ciliate, apex acuminate, appressed pubescent outside; pistillate inflorescences not seen. Staminate flowers c. 4 mm diam; pedicel c. 0.5 mm long, c. 0.3 mm diam, pubescent to puberulent; sepals 5, elliptic, 2-2.4 by 1-1.2 mm, base connate, margin entire, apex acute to acuminate, densely pubescent to puberulent outside; petals only 3 observed, but withered, elliptic, 1.4–1.6 by 0.7–1 mm, white, base connate, margin entire, apex acute, glabrous on both sides; disc lobes irregular, nearly semi-orbicular, 0.2-0.3 by c. 0.3 mm; stamens



Map 15 Distributions of *Trigonostemon angustifolius* Merr. (♠); *T. cumingii* Müll.Arg. (★); *T. stenophyllus* Quisumb. (■); *T. whiteanus* (Croizat) Airy Shaw (♠).

c. 9, arranged into 2 whorls, outer whorl 5, alternate with disc glands, opening introrse, free, filaments c. 0.15 mm long, inner whorl c. 4, opening more or less extrorse, connate into an androphore, hidden, c. 0.5 mm long, anthers ellipsoid, c. 0.6 mm long. *Pistillate flowers, fruits* and *seeds* unknown.

Distribution — Philippines (endemic).

Habitat & Ecology — Rugged country, on red clay soil. Altitude: 300 m. Flowering: June.

Note — A rare and poorly known species. The stamens are arranged into two whorls with c. 5 free outer and 4 inner connate ones, which seems typical for *Dimorphocalyx*, but the inflorescences are too much condensed. A molecular phylogenetic study is necessary to determine this species affiliation.

37. Trigonostemon stenophyllus Quisumb. — Map 15

Trigonostemon stenophyllus Quisumb. (1930) 330, f. 8. — Type: BS (Ramos & Edaño) 47331 (holo PNH†; iso A, K, NY*, UC*), Philippines, Luzon, Isabela Prov., Mount Moises.

Shrubs, up to 1 m tall; branches terete, 2-3.5 mm diam, pubescent when young, glabrous when mature. Stipules unknown. Leaves: petioles 1-4 cm long, somewhat pubescent; blade oblong to lanceolate, 5.5-16.5 by 1-2.5 cm, chartaceous, base acute to obtuse, margin entire to slightly distantly serrate, apex acuminate, upper surface brown to dark brown when dry, glabrous, lower surface paler and sparsely pubescent; midrib flat above and elevated beneath, nerves 6-11 pairs, veinlets reticulate. Inflorescences: staminate ones unknown; pistillate ones axillary, racemose, up to 5.5 cm long, pubescent; bracts narrowly lanceolate, 3–4 mm long. Staminate flowers unknown. Pistillate flowers c. 4.5 mm diam; pedicels slightly thickened towards apex, c. 9.5 mm long, apically c. 0.6 mm diam, appressed pubescent; sepals oblong to lanceolate, c. 3 by 0.7 mm, margin entire, apex acute to acuminate, appressed pubescent outside, glabrous inside; petals oblong-obovate, c. 5 by 2 mm, apex rounded, glabrous; disc lobes elliptic, c. 0.5 by 0.3 mm, apex rounded, glabrous; ovary c. 0.95 mm diam, densely pubescent; styles 0.1-0.2 mm long; stigma linear, c. 1.3 mm long, deeply bifid into 2 arms, each arm c. 1 mm long, slightly thickened near base. Fruits c. 1.2 cm diam, brown, sparsely puberulent, persistent sepals not accrescent; wall c. 0.35 mm thick, exocarp partly detaching. Seeds c. 7 mm diam.

Distribution — Philippines (endemic).

Note — The species is only known from the type. The description is based on Quisumbing (1930). Due to the insufficient specimen seen, especially the lack of staminate flowers, the species is regarded doubtful here. It is probably a synonym of *T. filiformis*.

38. *Trigonostemon whiteanus* (Croizat) Airy Shaw — Map 15

Trigonostemon whiteanus (Croizat) Airy Shaw (1983a) 68; (1983b) 48. — Cheilosa whiteana Croizat (1942b) 507; Airy Shaw (1963) 365, in note. — Type: FB (Curran) 17733 (holo A; iso K), Philippines, Luzon, Pampanga Prov., Mt Arayat.

Shrubs or trees; flowering branches c. 3 mm diam. *Bark* 0.3–0.4 mm thick, blackish, smooth, lenticellate, appressed pubescent when young, glabrous when mature; wood yellowish. *Stipules* not seen (see note 2). *Leaves*: petiole furrowed above, rounded beneath, 3–5.5 cm long, 1.2–1.5 mm diam (middle part), slightly thickened at base and apex, slightly pubescent above, glabrous beneath; blade broad ovate, 9–13 by 6.5–9 cm, thin coriaceous, base rounded, with 2 adaxial glands, slightly hairy, margin entire, apex acute to acuminate, yellowish green above (when dry), pinkish brown beneath, both sides glabrous; ve-

nations triplinerved, midrib slightly raised above and distinctly elevated beneath, nerves 4-7 pairs, curved, slightly raised on lower side, veinlets reticulate. Inflorescences: staminate ones not seen; pistillate ones few branched, pyramidal, densely appressed pubescent, up to 7 cm long and 2.5 mm diam; bracts triangular, 1.5-3 by 1-1.5 mm, apex acuminate, densely appressed pubescent outside, glabrous inside. Staminate flowers not seen. Pistillate flowers 3.5-4.5 mm diam; pedicel 4-6.5 mm long, 0.45-0.8 mm diam, appressed pubescent; sepals triangular to lanceolate, 2-2.5 by 0.8-1.2 mm, apex acuminate, appressed pubescent outside; petals fallen, remnants membranous, yellowish, glabrous; disc lobes c. 0.5 mm wide, appressed pubescent; ovary 2-2.2 mm diam, densely appressed pubescent; style c. 0.5 mm long, trifid, stigma 0.7-0.8 mm long, branches basally connate, apex very slightly thickened and bifid. Fruits and seeds unknown.

Distribution — Philippines (endemic).

Notes — 1. Only known from the type collection. No staminate flowers are available, which makes the generic identification uncertain, but the petals and trifid styles are typical for *Trigonostemon*, though not exclusively.

2. The development of the stipules seemed to be constrained, only two very obscure elevations with a few hairs were found instead of normal stipules.

EXCLUDED NAMES

Trigonostemon arboreus Ridl. (1928) 75. — Type: KEP (Nur or Henderson) 18595 (holo SING), Malay Peninsula, Pulau Tioman, Sedagong. = **Omphalea malayana** Merr. (Milne 1995a).

Trigonostemon asahanensis Croizat (1942a) 54. — Type: Rahmat Si Boeea 9872 (L), Sumatra, Asahan, vicinity of Tomoean Dolok. = **Dimorphocalyx muricatus** (Hook.f.) Airy Shaw (Van Welzen & Van Oostrum 2015).

Trigonostemon bulusanensis Elmer (1939) 3735; Airy Shaw (1967) 413. — Dimorphocalyx bulusanensis (Elmer) Airy Shaw (1972b) 92. — Type: Elmer 17296 (K, L), Philippines, Luzon, Prov. of Sorsogon, Irosin (Mt Bulusan). = Dimorphocalyx malayanus Hook.f. (Van Welzen & Van Oostrum 2015).

Trigonostemon forbesii Pax in Pax & K.Hoffm. (1911) 88; S.Moore (1925) 100; Jabl. (1963) 165. — Type: Forbes 1892 (GH, L), Indonesia, Sumatra, Lampong, Mt Tengamoes (= Gunung Tanggamus). = Wetria insignis (Steud.) Airy Shaw (Van Welzen 1998).

Tritraxis macrophylla Müll.Arg. (1864a) 482. — Trigonostemon macrophyllus (Müll.Arg.) Müll.Arg. (1865) 213. — Ostodes macrophylla (Müll.Arg.) Benth. ex Pax & K.Hoffm. (1911) 18; Ridl. (1924) 269, f. 153. — Type: Griffith 4788 (holo K), Malacca. = Paracroton pendulus (Hassk.) Miq. (Esser 2007).

Trigonostemon oliganthum K.Schum. in K.Schum. & Lauterb. (1905) 298. — Type: Nyman 554 (holo UPS), Kaiser-Wilhelmsland [= Papua New Guinea], Sattelberg. = Cleidion papuanum Lauterb. (Kulju & Van Welzen 2005).

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

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IDENTIFICATION LIST

1 = T. apetalogyne Airy Shaw

2 = T. aurantiacus (Kurz ex Teijsm. & Binn.) Boerl.

3 = T. balgooyi R.Y.Yu & Welzen

4 = T. beccarii Ridl.

5 = T. calcicolus (R.I.Milne) R.Y.Yu & Welzen

6 = T. capillipes (Hook.f.) Airy Shaw

7 = T. detritiferus R.I.Milne

8 = T. diffusus Merr.

9 = T. dipteranthus Airy Shaw

10 = T. filiformis Quisumb.

11 = T. flavidus Gagnep.

12 = T. hartleyi Airy Shaw

13a = T. laevigatus Müll.Arg. var. laevigatus

13b = T. laevigatus Müll.Arg. var. croceus (B.C.Stone) R.Y.Yu & Welzen

14 = T. longifolius Wall. ex Müll.Arg.

15 = T. longipes (Merr.) Merr.

16 = T. lychnos (R.I.Milne) R.Y.Yu & Welzen

17 = T. magnificus R.I.Milne

18 = T. malaccanus Müll.Arg.

19 = T. merrillii Elmer

20 = T. oblongifolius Merr.

21 = T. pentandrus Pax & K.Hoffm.

22 = T. philippinensis Stapf

23 = T. polyanthus Merr.

24 = T. rufescens Jabl.

25 = T. sandakanensis Jabl.

26 = T. scopulatus R.Y.Yu & Welzen

27 = T. serratus Blume

28 = T. sinclairii Jabl.

29a = T. verticillatus (Jack) Pax var. verticillatus

29b = T. verticillatus (Jack) Pax var. salicifolius (Ridl.) Whitmore

30 = T. victoriae R.Y.Yu & Welzen

31a = T. villosus Hook.f. var. villosus

31b = T. villosus Hook.f. var. borneensis (Merr.) Airy Shaw

31c = T. villosus Hook.f. var. cordatus R.Y.Yu & Welzen

31d = T. villosus Hook.f. var. merrillianus (Airy Shaw) R.Y.Yu & Welzen

32a = T. viridissimus (Kurz) Airy Shaw var. viridissimus

32b = T. viridissimus (Kurz) Airy Shaw var. elegantissimus (Airy Shaw) Airy Shaw

33 = T. wetriifolius Airy Shaw & Ng

34 = T. wildeorum R.Y.Yu & Welzen

doubtful 35 = T. angustifolius Merr. doubtful 36 = T. cumingii Müll.Arg.

doubtful 37 = T. stenophyllus Quisumb.

doubtful 38 = T. whiteanus (Croizat) Airy Shaw

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