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Contents

Chapter 1 General Introduction

This dissertation studies four aspects of the plant genus *Trigonostemon* Blume (Euphorbiaceae): the taxonomy, pollen morphology, molecular phylogeny and historical biogeography. The background of the research, limitations in the previous studies and an outline of the dissertation are provided in this chapter.

Background: the family Euphorbiaceae and the genus *Trigonostemon*

The plant family Euphorbiaceae is one of the most morphologically diverse groups among the Angiosperms. The family (sensu APG IV 2016, see below) contains 218 genera and c. 6700 species (Stevens 2001 onwards). A diagnostic set of characters applying to all Euphorbiaceae is lacking. There are a few characters that in combination are more or less typical of the majority of genera and species, e.g., the presence of stipules, a superior ovary and a rhegma (an often explosively dehiscing fruit, where only the columella remains), but exceptions are rampant (except the superior ovary). The exact circumscription of the Euphorbiaceae varied enormously through the ages, many small families have been included or excluded, see Radcliffe-Smith (1987) for an overview (e.g., Buxaceae, Daphniphyllaceae, Stilaginaceae). With the advancement of APG, the order Malpighiales, in which the Euphorbiaceae are classified, proved to be difficult to solve phylogenetically. Presently (APG IV 2016; Figure 1), the Euphorbiaceae are split in various families. For the Pandaceae and Putranjivaceae, two morphologically rather different families, it is now clear that they are not closely related to the Euphorbiaceae. The former subfamilies with two ovules per locule now form the Phyllanthaceae and Picrodendraceae (sister clades in APG IV). The subfamilies with one ovule per locule (Acalyphoideae, Crotonoideae, Euphorbioideae) formed at first the Euphorbiaceae in the strict sense, till it became obvious that the Rafflesiaceae form a clade just above the basal clade of the Euphorbiaceae (Wurdack & Davis 2009). The parasitic Rafflesiaceae have inferior ovaries with many ovules per locule, uniting them with the Euphorbiaceae would not only mean that a well-recognisable family will disappear (Rafflesiaceae), but also that the Euphorbiaceae will lack any diagnostic characters. Therefore, the basal Peroideae clade (Wurdack et al. 2005) is now accepted as the separate family Peraceae (APG IV 2016), next to the Rafflesiaceae and Euphorbiaceae.

Trigonostemon was established by Blume in 1825. The genus name refers to the stamens that form a triangle when seen from above. It includes a total of 59 species (Chapter 4), ranging from S India and Sri Lanka to S China, throughout mainland SE Asia and Malesia to NE Australia and the W Pacific (Govaerts et al. 2000; Map 1). The genus has always been classified in the subfamily Crotonoideae. There are four clades in the Crotonoideae based on the molecular phylogeny of Wurdack et al. (2005), the upper two (marked as C1 and C2 in Wurdack et al. 2005) are characterised by inaperturate pollen grains. *Trigonostemon* is the largest genus in the C2 clade within the polytomy of 25 other genera including *Ostodes* Blume (Figure 2), which is often considered to be closely related to *Trigonostemon*. *Dimorphocalyx* Thwaites was not included in the phylogeny, although it was also considered to be a close relative of *Trigonostemon* and *Ostodes*. Among the various genera, *Trigonostemon* can be recognised mainly by having colourful petals in both staminate and pistillate flowers and 3 or 5 connate stamens (Figure 40).

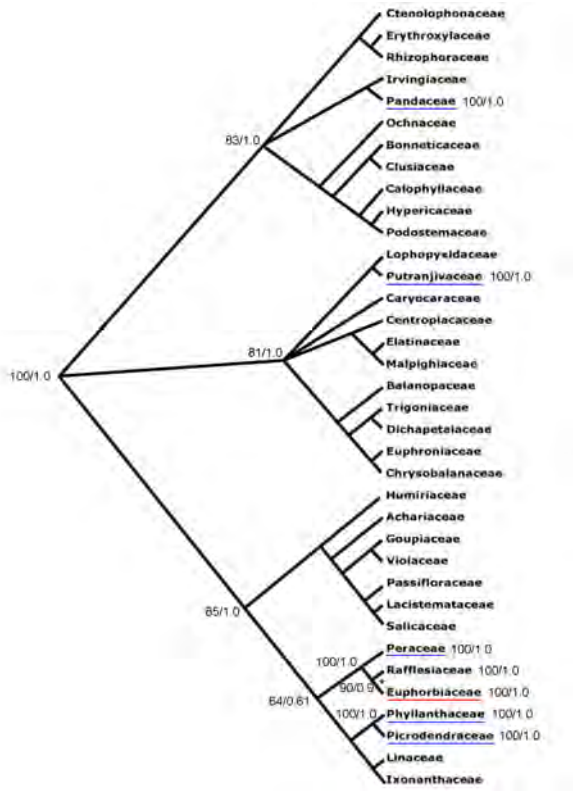
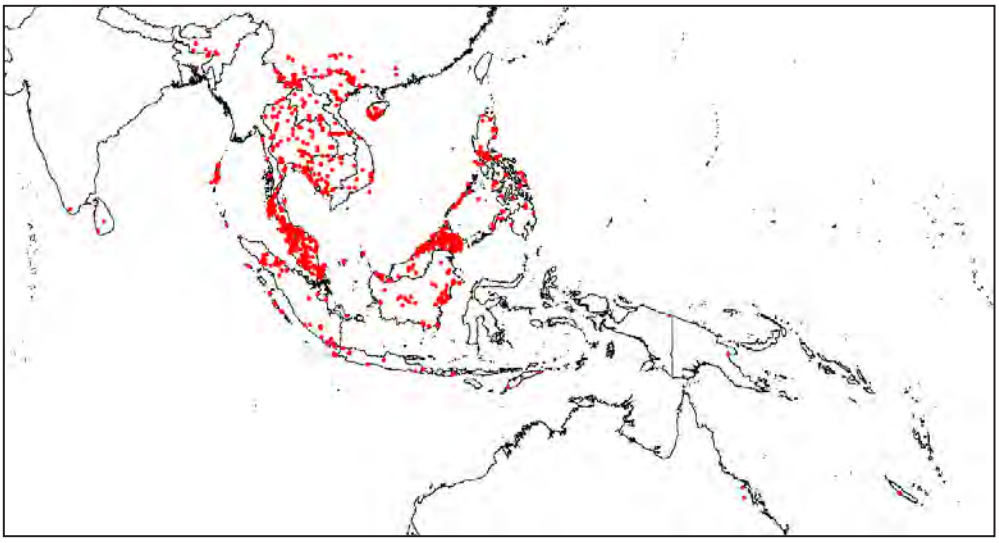


Figure 1 Phylogenetic position of the Euphorbiaceae (marked with a red line) and its close relatives within the Malpighiales. The figure is modified from Stevens (2001 onwards). Families split from the traditional Euphorbiaceae (sensu Pax 1890) are marked with blue lines. The Maximum Likelihood bootstrap values/Bayesian posterior probabilities are given for the relevant nodes. The supporting values of the crown node (marked with an asterisk) of the Rafflesiaceae and Euphorbiaceae are based on Wurdack & Davis (2009), other values are based on Xi et al. (2012).

Limitations in previous studies

Trigonostemon is a difficult group in taxonomy. In identification keys it is generally keyed out negatively, always at the end of blocks and often in various blocks (e.g., van Welzen 2005). Within the genus, more than 140 taxa have been described (Govaerts et al. 2000), but the species delimitation has always been blurred and problematic. On the one hand, there is a limitation in the use of the floral characters in species delimitation; on the other hand, massive variation exists in the vegetative characters (for the taxonomic history and a detailed discussion of characters see Chapter 2). It is often difficult for botanists to decide whether a character is useful without studying the whole genus. As a result, many species were described merely based on extreme forms in a continuous variation. A comprehensive revision was urgently needed, in which the variation in all characters would be carefully examined and evaluated and all species would be revised by the same criteria.

Pollen morphology often provides extra evidence for taxonomy (Erdtman 1952). *Trigonostemon* pollen has hardly been studied before, but in the only literature (Punt 1962) a unique type of exine ornamentation was found. The ‘croton pattern’ ornamentation is a key character in the



Map 1 Distribution of *Trigonostemon*. Red dots refer to georeferenced specimen records from various herbaria.

pollen of Crotonoideae and a few other taxa (Punt 1962; Nowicke 1994), but the pollen of some *Trigonostemon* species was shown to have a verrucate exine. This is possibly indicative of an evolutionary change, but before concrete conclusions could be made, a more extensive exploration of the pollen morphology of the whole genus was needed.

Although it is clear that *Trigonostemon* (one whorl of 3 or 5 stamens) should be classified in the subfamily Crotonoideae, opinions are divided as to its generic circumscription: Müller (1865, 1866) merged *Dimorphocalyx* (Thwaites 1861; two whorls of 7–20 stamens, Figure 40k) and *Tritaxis* Baill. (Baillon 1858; three whorls of c. 13 stamens, for illustration see Gagnepain 1925b) with *Trigonostemon* into a *Trigonostemon sensu lato*; other botanists, e.g., Bentham (1878, 1880) and Pax (1890), treated *Trigonostemon* strictly according to Blume's concept (1825). Furthermore, the previous infrageneric classifications of *Trigonostemon* (for a detailed review of the infrageneric classifications see Chapter 2) are problematic. They only relied on morphological characters of a limited number of species, and contained several cases of misidentification and misplacement.

Phylogenetic systematics has the potential to solve these problems. Compared to classical taxonomy, the cladistic approach (Hennig 1965) incorporates evolutionary theory in its methodology by discriminating between primitive and derived homologous character states (though the discrimination of characters and their states can be subjective). Taxa are considered phylogenetically related because of shared derived characters. This provides a relatively more objective way to select useful characters compared to classical taxonomy. The selection of characters (and how much weight to put on each selected character) is also critical in classical taxonomy, but it is based on comparative morphology (van Steenis 1957) and depends heavily on one's (subjective) experience. Nucleotide sequences in the plant genome provide a much larger amount of data (characters) to evaluate the similarity between taxa, and the subjectivity has changed to the alignment phase to establish which parts of the sequences are homologous. The results obtained by molecular data can also be used to analyse and interpret the changes in macromorphology and pollen morphology.

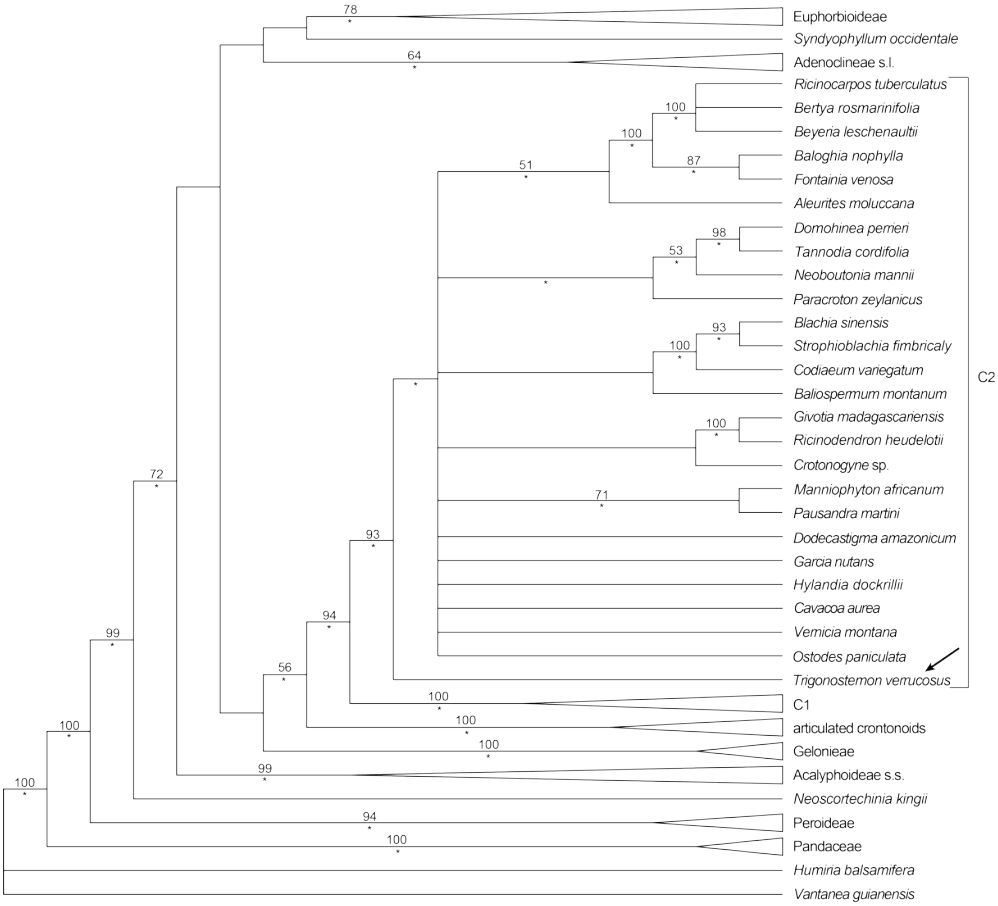


Figure 2 Phylogenetic position of *Trigonostemon* (marked with an arrow) within the C2 clade of the Crotonoideae. The figure is modified from Wurdack et al. (2005). The Maximum Likelihood bootstrap values are indicated above the branches if the values are above 50%; the asterisks below the branches indicates a Bayesian posterior probability above 0.95.

Trigonostemon has a typical Southeast Asian distribution. This area comprises six of the 25 biodiversity hotspots identified by Myers et al. (2000). Most species of *Trigonostemon* are found in the Flora Malesiana region (van Steenis 1950; Raes & van Welzen 2009), which contains one of the world's richest floras (42,000 vascular plant species as estimated by Roos (1993), or even up to 45,000 species as estimated by Corlett & Primack (2011)). The migration routes (particularly those across the Wallace's line; van Welzen et al. 2011 and references therein) of plants and animals in this area have always been a subject of great interest in biogeography, but the general migration patterns can only be discovered when a sufficient number of case studies are performed. *Trigonostemon* can provide a good addition to this research subject, because its distribution covers all SE Asian regions with the only exception of Sulawesi. Previous studies have shown that the Philippines often acted as a stepping stone for the migrations between West and East Malesia (e.g., Nauheimer et al. 2012, Thomas et al. 2012). The migration routes of *Trigonostemon* can be used to compare with the previous studies and evaluate this conclusion.

Outline of this dissertation

Chapters 2–4 are taxonomic revisions of *Trigonostemon*. These chapters only deal with the species within *Trigonostemon sensu stricto* (Blume 1825), aiming to correct the previous nomenclatural errors, and to provide a reliable delimitation between the species. These chapters serve as the basis of the following chapters. Species boundaries were determined by morphological discontinuities (i.e., the 'morphological species concept'). Expressions of this concept can be found in e.g., Linnaeus 1736, 1754, Lindley 1832, Bentham 1875, Gray 1887, Du Rietz 1930, Davis & Heywood, 1963 and Cronquist 1978. In practice, both the differences and similarities (the two phases of 'analysis' and 'synthesis' as argued by van Steenis 1957) among specimens were always taken into account. Chapter 2 does not include data obtained from the field work in the Philippines. This field trip could continue somewhat unexpectedly, and resulted in many new data for various species that were poorly understood from herbarium material. This necessitated a new article (Chapter 3), in which the descriptions of the relevant species were updated. Time, normally limited, permitted the final revision of the non-Malesian species of the genus, mainly found in the Indian subcontinent, Indochina and South China. The results can be found in Chapter 4.

Chapter 5 is an exploration of the pollen morphology of *Trigonostemon* and its close relatives, aiming to gain insight in the delimitation and infrageneric classification of *Trigonostemon*. The pollen of various species often has a different degree of resistance to acetolysis. Whether the anther is mature or not also affects the pollen morphology. Pollen of young flowers tends to have closed lumina. When assessing the variation, deformed or too young pollen grains were not used to avoid bias. *Trigonostemon* appeared to have two main types of pollen (one type that could be subdivided into two). The next chapter explains the correlations between these pollen types and the molecular phylogeny.

Chapter 6 reconstructs the phylogenies of *Trigonostemon* and its close relatives using five molecular markers (the nuclear ITS and chloroplast *trnK* intron, *trnT-L*, *trnL-F* and *rbcL* sequences). This is the core chapter, aiming to (1) confirm the systematic position of *Trigonostemon* in the Euphorbiaceae, (2) clarify the generic delimitation of *Trigonostemon* and its relatives/look-alikes (i.e., *Dimorphocalyx*, *Tritaxis* and *Ostodes*), (3) interpret the evolutionary trends in *Trigonostemon* in reference to the pollen morphology and (4) revise the infrageneric classification of the genus. About two third of the species of *Trigonostemon* were represented in the analyses. The molecular phylogenies were inferred by maximum parsimony, maximum likelihood and Bayesian methods. Characters in morphology and pollen morphology were mapped on the phylogeny to visualize their evolutionary trends. Because the phylogeny will clarify the generic boundaries, one might argue that it would have been better to have the phylogenetic analyses before the taxonomic revisions, but the single species are the actual entities in the analyses, and it was necessary to have a clear species concept before reconstructing the phylogenies.

Chapter 7 builds on the previous chapter. Historical biogeographic analyses of the genera *Trigonostemon* and *Dimorphocalyx* are made, in order to investigate their geographical origin and dispersal routes, and to provide an explanation for the rapid diversification in sect. *Trigonostemon* from a historical biogeographic angle. A Bayesian dating analysis was performed to infer the divergence times of the nodes, and the ancestral areas were optimised using a likelihood analysis under the Dispersal-Extinction-Cladogenesis (DEC) model and a Statistical Dispersal-Vicariance analysis (S-DIVA). The dispersal/vicariance events were discussed in light of the tectonic history of SE Asia, and the historical biogeography was reconstructed.

Chapter 2 A taxonomic revision of *Trigonostemon* (Euphorbiaceae) in Malesia

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Abstract *Trigonostemon* is taxonomically revised for Malesia based on herbarium collections and field observations. Thirty-eight species are recognised 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. Identification keys, nomenclature, descriptions, typification, geographic distributions and taxonomic notes are provided.

Key words

Euphorbiaceae
Malesia
morphological revision
taxonomy
Trigonostemon

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 species *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. Because of the obscure status of *Enchidium* and the wide use of the name *Trigonostemon*, van Steenis (1948a, 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 of the type species, *T*. *serratus* Blume. More than 140 scientific names were published within the genus *Trigonostemon* over the years.

Besides *Trigonostemon*, 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. (formerly *Dimorphocalyx* Thwaites; comprising the type *D*. *glabellus* as a synonym of ***T***. ***lawianus*** (Nimmo) 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 transferred to *Paracroton* Miq. by Esser (2007) and by Balakrishnan & Chakrabarty (1993), respectively);

Sect. 3. *Tritaxis* (Baill.) Müll.Arg. (formerly *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. (formerly *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 Baill., *T*. *nemoralis* Thwaites, ***T***. ***serratus***);
Sect. 7. *Silvaea* (Hook. & Arn.) Müll.Arg. (formerly *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.

Opposed to Müller Argoviensis (1865, 1866), Bentham (1878, 1880) and Hooker (1887) regarded the *Trigonostemon* as a genus 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, the petals in pistillate flowers are actually 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, 1912b, c, 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 *Trig*. *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) had an eclectic opinion on the delimitation of the genus as compared to the previous authors. Like Bentham and Hooker's (Bentham 1878, 1880, Hooker 1887) and Pax and Hoffmann's systems (Pax 1890, Pax & Hoffmann 1911, 1912b, c, 1914, 1919, 1931), he treated *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 in the Malay Peninsula, Sumatra and Borneo. He recorded 26 species, but only 12 species were based on complete material and very few of them had 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*. *pentandrus**, *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 1982a), New Guinea (Airy Shaw 1980b). Most of these contributions lack proper descriptions. Milne (1994, 1995a) revised the genus, but merely described new entities and 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 infrageneric classification are pointed out. An infrageneric 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 plants are always densely hairy in the young parts (e.g., branchlets and buds) 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* by the densely hairy upper surface of the leaf blades, and *T*. *rufescens* and *T*. *sinclairii* are both distinct species 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 recognised 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 characterised 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 the 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 glabrous and more slender than that of pistillate flowers, which is 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 species have sepals with a subapical gland outside and this was used as a 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 present near the base. 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 more or less correlates with that of the staminate flowers. If the disc in the staminate flowers is annular, then it is often also annular in the pistillate flowers; if glandular in the staminate ones, then variable, glandular or annular, in the 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 always gather 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*. 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 divarication in the anthers is a good character to use in a future infrageneric classification, but this should be based on mature stamens as the it 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 infrageneric 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.

TAXONOMY

Throughout this part, an asterisk refers to a specimen seen as image.

Trigonostemon Blume

Trigonostemon Blume, Bijdr. (1825) 600 (‘*Trigostemon*’); Fl. Javae (1828) Preface 8 (name corrected in note), nom. cons.; Baill., Étude Euphorb. (1858) 340, pl. 11, f. 12; Müll.Arg. Linnaea 34 (1865) 212; in A.DC., Prodr. 15, 2 (1866) 1105; Benth. in Benth. & Hook.f., Gen. Pl. 3 (1880) 298; Hook.f., Fl. Brit. India 5 (1887) 395; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 84; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 85; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 451; Ridl., Fl. Malay Penins. 3 (1924) 263; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1925b) 309; Pax & K.Hoffm. in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169; Jabl., Brittonia 15 (1963) 151; Backer & Bakh.f., Fl. Java 1 (1963) 495; Airy Shaw, Kew Bull. 26 (1972a) 344; Whitmore, Tree Fl. Malaya 2 (1973) 134; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 201; Kew Bull. 32 (1978) 415; Kew Bull. 35 (1980a) 690; Kew Bull., Addit. Ser. 8 (1980b) 205; Kew Bull. 36 (1981) 352; Kew Bull. 37 (1982a) 36; Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 46; G.L.Webster, Ann. Missouri Bot. Gard. 81 (1994) 108; R.I.Milne, Kew Bull. 49 (1994) 445; Kew Bull. 50 (1995a) 25; Kew Bull. 50 (1995b) 51; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 162; Philcox in Dassan., Fl. Ceyl. 11 (1997) 110; Radcl.-Sm., Gen. Euphorbiacearum (2001) 307; Chantar.,Thai Forest Bull. (Bot.) 33 (2005) 21; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 573; P.T.Li & M.G.Gilbert. in C.Y.Wu, P.H.Raven & D.Y.Hong, Fl. China 11 (2008) 272; G.L.Webster in Kubitzki, Fam. & Gen. Vasc. Pl. 11 (2014) 171. — *Trigonostemon* Blume sect. *Eutrigonostemon* Müll.Arg., Linnaea 34 (1865) 214, nom. inval.; in A.DC., Prodr. 15, 2 (1866) 1108; Benth., J. Linn. Soc., Bot. 17 (1878) 224; in Benth. & Hook.f., Gen. Pl. 3 (1880) 298; Hook.f., Fl. Brit. India 5 (1887) 396; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 84; Pax & K.Hoffm. in

Engl., Pflanzenr. IV.147.iii (1911) 88; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169. — *Trigonostemon* Blume sect. *Trigonostemon*: Jabl., Brittonia 15 (1963) 158. — Type: *Trigonostemon serratus* Blume.

Enchidium Jack, Malayan Misc. 2 (1822) 89, nom. rej.; Baill., Étude Euphorb. (1858) 652; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1256 ('*Enchidion*'); Merr., J. Arnold Arbor. 33 (1952) 224. — Type: *Enchidium verticillatum* Jack [= *Trigonostemon verticillatus* (Jack) Pax].

Silvaea Hook. & Arn., Bot. Beechey Voy. (1837) 211, non Phil., Fl. Atacam. (1860) 21, nec Meisn. in A.DC., Prodr. 15, 1 (1864) 84; Baill., Étude Euphorb. (1858) 341. — *Trigonostemon* Blume sect. *Silvaea* (Hook. & Arn.) Müll.Arg., Linnaea 34 (1865) 214; in A.DC., Prodr. 15, 2 (1866) 1110. — Type: *Silvaea semperflorens* (Roxb.) Hook. & Arn. [= *Trigonostemon semperflorens* (Roxb.) Müll.Arg.].

Athroisma Griff., Not. Pl. Asiat. 4 (1854a) 477, nom. inval., non DC. in Guillem., Arch. Bot. (Paris) 2 (1833) 516. — Syntypes: *Athroisma dentatum* Griff. [=? *Trigonostemon longifolius* Wall. ex Baill.; 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 Baill.; see Airy Shaw 1972a: 347].

Telogyne Baill., Étude Euphorb. (1858) 327, pl. 11, f. 13. — *Trigonostemon* Blume sect. *Telogyne* (Baill.) Müll.Arg., Linnaea 34 (1865) 214; in A.DC., Prodr. 15, 2 (1866) 1107; Benth., J. Linn. Soc., Bot. 17 (1878) 225; in Benth. & Hook.f., Gen. Pl. 3 (1880) 298; Hook.f., Fl. Brit. India 5 (1887) 398; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 84; Pax & K.Hoffm. in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169; Jabl., Brittonia 15 (1963) 152. — Type: *Telogyne indica* Baill. [= *Trigonostemon verticillatus* (Jack) Pax].

Tylosepalum Kurz ex Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 27 (1864) 50. — *Codiaeum* A.Juss. sect. *Tylosepalum* (Kurz ex Teijsm. & Binn.) Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1117. — *Trigonostemon* Blume sect. *Tylosepalum* (Kurz ex Teijsm. & Binn.) Pax & K.Hoffm. in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169; Jabl., Brittonia 15 (1963) 163. — Type: *Tylosepalum aurantiacum* Kurz ex Teijsm. & Binn. [= *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl.].

Trigonostemon Blume sect. *Pycnanthera* Benth., J. Linn. Soc., Bot. 17 (1878) 244; in Benth. & Hook.f., Pl. Gen. 3 (1880) 299; Hook.f., Fl. Brit. India 5 (1887) 398; Pax in Engl. & Prantl, Nat. Pflanzenfam. 3, 5 (1890) 84; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 92; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169. — Lectotype (designated here): *Trigonostemon diplopetalus* Thwaites.

Nepenthandra S.Moore, J. Bot. 43 (1905) 149. — Type: *Nepenthandra lanceolata* S.Moore [= *Trigonostemon lanceolatus* (S.Moore) Pax].

Actephilopsis Ridl., Bull. Misc. Inform. Kew (1923) 360. — Type: *Actephilopsis malayana* [= *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl.].

Trigonostemon Blume sect. *Dichotomae* Merr., Univ. Calif. Publ. Bot. 10 (1924) 425; Pax & K.Hoffm. in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169. — Type: *Trigonostemon petelotii* Merr. [= *Trigonostemon laevigatus* Müll.Arg.].

Prosartema Gagnep., Bull. Soc. Bot. France 71 (1924b) 875; in Lecomte, Fl. Indo-Chine 5 (1925b) 304. — Type: *Prosartema stellaris* Gagnep. [= *Trigonostemon stellaris* (Gagnep.) Airy Shaw].

Poilaniella Gagnep., Bull. Soc. Bot. France 72 (1925a) 467; in Lecomte, Fl. Indo-Chine 5 (1925b) 307. — Type: *Poilaniella fragilis* [= *Trigonostemon fragilis* (Gagnep.) Airy Shaw].

Neotrigonostemon Pax & K.Hoffm., Notizbl. Bot. Gart. Berlin-Dahlem 10 (1928) 385; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169. — Type: *Neotrigonostemon diversifolius* Pax & K.Hoffm. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].

Kurziodendron N.P.Balakr., Bull. Bot. Surv. India 8 (1966) 68. — Type: *Kurziodendron viridissimum* (Kurz) N.P.Balakr. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].

Shrubs to trees, monoecious; branches terete, sometimes hollow, often with leaf scars, rarely with adventitious roots (*T. detritiferus*, *T. wetriifolius* Airy Shaw & Ng and *T. sandakanensis* Jabl.); buds densely hairy. *Indumentum* of simple hairs (*T. balgooyi* and *T. reidioides* also stellately bundled hairs), dense in 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 distantly 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 reflexed at apex; stamens 3 or 5, filaments united into an erect androphore, latter sometimes 3- or 5-cleft at top, anthers ellipsoid, either on a 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* appressed 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

2. Stem not branched (plant monocaul) 3
2. Stem branched 5

3. Inflorescences longer than 7 cm; flowers never cauliflorous. — Sabah: Sandakan, Kabili-Sepilok FR ..... 25. *T. sandakanensis*
3. Inflorescences shorter than 7 cm; flowers partly cauliflorous. — Malay Peninsula and Brunei 4

4. Flowers reddish purple; stamens 3. — Brunei: Temburong ..... 7. *T. detritiferus*
4. Flowers yellow; stamens 5. — Malay Peninsula: Lesong FR ..... 33. *T. wetriifolius*

5. Leaf blades densely hairy on upper side ..... 11. *T. flavidus*
5. Leaf blades glabrous on upper side (or slightly hairy when young) 6

6. Staminate flowers in cauliflorous fascicles, directly on stems 7
6. Staminate flowers never cauliflorous, in racemes or thyrses 8

7. Flowers orange; stamens 3; pistillate inflorescences being subtended by big leaf-like bracts. — Malay Peninsula, Sumatra, Java, Bali ..... 2. *T. aurantiacus*
7. Flowers purplish black; stamens 5; pistillate inflorescences absent, bracts small. — Sumatra: Alas River area ..... 34. *T. wildeorum*

8. Inflorescences (staminate ones if unisexual) racemose thyrses (no side branches) 9
8. Inflorescences (staminate ones if unisexual) paniculate thyrses (branching) 11

9. Young branches with reddish annular stripes. — Java ..... 27. *T. serratus*
9. Young branches without reddish annular stripes. — Malay Peninsula, Sumatra, Java, Borneo, Philippines 10

10. Stamens 5; fruits not warty. — Sumatra ..... 4. *T. beccarii*
10. Stamens 3; fruits warty. — Malay Peninsula, Sumatra, Java, Borneo, Philippines ..... 14. *T. longifolius*

11. Petals elliptic or spathulate; stamens 5, anthers divaricate ..... 6. *T. capillipes*
11. Petals flabellate and bilobed; stamens 3, anthers parallel ..... 13. *T. laevigatus*

12. Leaf blades hairy on upper side when mature 13
12. Leaf blades glabrous on upper side when mature 17

13. Stamens 3 14
13. Stamens 5 16

14. Pistillate sepals greatly accrescent in fruits. — Malay Peninsula ..... 28. *T. sinclairii*
14. Pistillate sepals not much accrescent. — Sabah, Philippines 15

15. Staminate inflorescences paintbrush-like glomerules along rachis. — Philippines ..... 19. *T. merrillii*
15. Staminate inflorescences racemes or thyrses (a few flowers per node along rachis). — Sabah ..... 31c. *T. villosus* var. *cordatus*

16. Plant with stellately bundled hairs all over (except on the upper surfaces of leaves, bracts and sepals). — Malay Peninsula: Endau Rompin and Gunung Panti ..... 3. *T. balgooyi*
16. Plant with only simple hairs. — Malay Peninsula: Mawai – Jemaluang Road ..... 24. *T. rufescens*

17. Staminate flowers in glomerules 18
17. Staminate flowers (sometimes mixed with pistillate flowers) in racemose or paniculate thyrses (not glomerulate) 23

18. Each glomerule with at most 1 bract.....19
18. Glomerules subtended by 2 or more bracts 22

19. Stamens 3.....20
19. Stamens 5.....21

20. Petioles up to 3.5 cm long. Inflorescences without leaf-like bracts. — Philippines .....
.....20. *T. oblongifolius*
20. Most petioles longer than 3.5 cm. Inflorescences with leaf-like bracts. — Borneo, Philippines .....31d. *T. villosus* var. *merrillianus*

21. Leaves larger than 16 by 6 cm. — Sarawak.....5. *T. calcicolus*
21. Leaves smaller than 16 by 6 cm. — Philippines.....15. *T. longipes*

22. Stamens 5. — Sumatra .....9. *T. dipteranthus*
22. Stamens 3. — Brunei.....16. *T. lychnos*

23. Inflorescences not branched (no side-branches).....24
23. Inflorescences branched.....32

24. Maximum petiole length less than 5.5 cm.....25
24. Maximum petiole length more than 5.5 cm.....28

25. Pistillate flowers single per inflorescence; pistillate sepals accrescent 26
25. Pistillate flowers more than 1 per inflorescence; pistillate sepals not accrescent 27

26. Leaf blades linear to long-lanceolate. — Sabah, Philippines .....10. *T. filiformis*
26. Leaf blades elliptic. — Philippines: Victoria Mountains..... 30. *T. victoriae*

27. More (often much more) than 4 pistillate flowers present on inflorescences; fruits warty ...
.....14. *T. longifolius*
27. Fewer than 4 pistillate flowers present on inflorescences; fruits smooth.....
.....31b. *T. villosus* var. *borneensis*

28. Stamens 3.....29
28. Stamens 5.....31

29. Inflorescences mainly unisexual. — Malay Peninsula, Sumatra .....18. *T. malaccanus*
29. Inflorescences bisexual. — Malay Peninsula 30

30. Ovary glabrous .....26. *T. scopulatus*
30. Ovary hairy ..... 31a. *T. villosus* var. *villosus*

31. Flowers pink; petals slightly bilobed. — Malay Peninsula: Gunung Angsi.....
.....21. *T. pentandrus*
31. Flowers dark reddish; petals entire. — Malay Peninsula.....29. *T. verticillatus*

32. Inflorescences branched not more than once.....33
32. Inflorescences branched two or more times.....36

33. Stamens 3.....34
33. Stamens 5.....35

34. Petals entire, dark yellow. — New Guinea.....1. *T. apetalogyne*
34. Petals bilobed, yellow or reddish. — Malay Peninsula, Sumatra, Java, Borneo, Philippines, Lesser Sunda Islands .....13. *T. laevigatus*

35. Pistillate sepals accrescent. — Malay Peninsula.....6. *T. capillipes*
35. Pistillate sepals not accrescent. — New Guinea .....12. *T. hartleyi*

36. Main rachis of inflorescences shorter than 10 cm 37
36. Main rachis of inflorescences longer than 10 cm 38

37. Stamens 5. — Malay Peninsula .....6. *T. capillipes*
37. Stamens 3. — Philippines.....23. *T. polyanthus*

38. Leaves triplinerved .....32. *T. viridissimus*
38. Leaves penninerved 39

39. Inflorescences often with very few flowers at one time. — Sarawak..... 8. *T. diffusus*
39. All flowers on the inflorescences open at once. — Malay Peninsula, Sumatra, Borneo, Philippines 40

40. Branchlets and lower side of leaf blades densely hairy. — Sumatra: Sikunder FR.....
.....17. *T. magnificus*
40. Branchlets and lower side of leaf blades glabrous. — Malay Peninsula, Sumatra, Borneo, Philippines .....22. *T. philippinensis*

REGIONAL KEYS

Key to the species of the Malay Peninsula

1. Petioles shorter than 3.5 cm long and shorter than 1/10 length of blade 2
1. Petioles more than 3.5 cm long or longer than 1/10 length of blade 8

2. Plants not branching; adventitious roots present. — Lesong FR.....33. *T. wetriifolius*
2. Plants branching; adventitious roots absent.....3

3. Leaves densely hairy above .....11. *T. flavidus*
3. Leaves glabrous or very slightly hairy above 4

4. Venation triplinerved (basal veins distinct from others), lateral veins often fewer than 9 pairs.....5
4. Venation penninerved (basal veins identical to others), lateral veins often more than 9 pairs.....6

5. Leaves and petiole totally glabrous .....13. *T. laevigatus*
5. Leaves slightly hairy beneath, petiole hairy.....32a. *T. viridissimus* var. *viridissimus*

6. Inflorescences not branched, often much longer than 8 cm ..... 14. *T. longifolius*
6. Inflorescences branched, less than 8 cm long 7

7. Staminate flowers cauliflorous; stamens 3 ..... 2. *T. aurantiacus*
7. Staminate flowers in axillary thyrses; stamens 5 ..... 6. *T. capillipes*

8. Leaf blades hairy 9
8. Leaf blades glabrous or very slightly hairy when young 13

9. Petiole and midrib with 2 layers of hairs, upper layer stiff, lower layer soft 10
9. Petiole and midrib with 1 layer of hairs 12

10. Lower layer hairs on petiole and midrib stellately bundled ..... 3. *T. balgooyi*
10. Lower layer hairs on petiole and midrib single 11

11. Inflorescences less than 3 cm long, stamens 5 ..... 24. *T. rufescens*
11. Inflorescences (often far) more than 3 cm long, stamens 3 ..... 28. *T. sinclairii*

12. Inflorescences of two forms, grouped at apex or clustered around branches (cauliflorous) ..... 26. *T. scopulatus*
12. Inflorescences of only one form, never grouped, never cauliflorous ..... 31a. *T. villosus* var. *villosus*

13. Inflorescences large panicles ..... 22. *T. philippinensis*
13. Inflorescences racemes or racemose thyrses 14

14. Inflorescences racemes; stamens 5. — Gunung Angsi ..... 21. *T. pentandrus*
14. Inflorescences racemose thyrses; stamens 3 ..... 18. *T. malaccanus*

Key to the species of Sumatra

1. Petioles less than 3.5 cm long 2
1. Petioles more than 3.5 cm long 8

2. Venation triplinerved (basal veins distinct from others), lateral veins often fewer than 9 pairs 3
2. Venation penninerved (basal veins identical to others), lateral veins often more than 9 pairs 4

3. Leaves and petiole totally glabrous ..... 13. *T. laevigatus*
3. Leaves slightly hairy beneath, petiole hairy ..... 32a. *T. viridissimus* var. *viridissimus*

4. Inflorescences (often far) more than 7 cm long ..... 14. *T. longifolius*
4. Inflorescences less than 7 cm long 5

5. Stamens 3 6
5. Stamens 5 7

6. Flowers orange ..... 2. *T. aurantiacus*
6. Flowers purplish black ..... 34. *T. wildeorum*

7. Inflorescences thyrses, auxillary or terminal; pistillate flowers at the end of rachis, pedicel c. 6 mm long, sepals very lightly pubescent ..... 4. *T. beccarii*
7. Inflorescences absent; pistillate flowers solitary and cauliflorous, pedicel c. 1 mm long, sepals densely hirsutulous to sericeous ..... 34. *T. wildeorum*

8. Inflorescences panicles, much branched 9
8. Inflorescences (racemose) thyrses or single glomerules, not branched..... 10

9. Leaf blade densely pubescent, flowering branches tomentose..... 17. *T. magnificus*
9. Leaf blade glabrous, flowering branches glabrescent ..... 22. *T. philippinensis*

10. Inflorescences glomerules, subtended by two large leaf-like bracts..... 9. *T. dipteranthus*
10. Inflorescences racemose thyrses, without leaf-like bracts..... 18. *T. malaccanus*

Key to the species of Java

1. Venation triplinerved (basal veins distinct from others), lateral veins often fewer than 9 pairs 2
1. Venation penninerved (basal veins identical to others), lateral veins often more than 9 pairs 3

2. Leaves and petiole totally glabrous ..... 13. *T. laevigatus*
2. Leaves slightly hairy beneath, petiole hairy..... 32a. *T. viridissimus* var. *viridissimus*

3. Young branches without reddish annular stripes; staminate flowers cauliflorous..... ..... 2. *T. aurantiacus*
3. Young branches with reddish annular stripes; staminate flowers in racemes .... 27. *T. serratus*

Key to the species of Borneo

1. Venation triplinerved (basal veins distinct from others), lateral veins often fewer than 9 pairs 2
1. Venation penninerved (basal veins identical to others), lateral veins often more than 9 pairs 3

2. Inflorescences shorter than 4 cm long ..... 13. *T. laevigatus*
2. Inflorescences longer than 4 cm long..... 32. *T. viridissimus*

3. Petiole shorter than 2.5 cm or shorter than 1/10 length of leaf blade..... 4
3. Petiole longer than 2.5 cm and longer than 1/10 length of leaf blade 8

4. Flowers partly cauliflorous, inflorescences shorter than 7 cm 5
4. Flowers never cauliflorous, inflorescences longer than 7 cm 7

5. Plants not branched, adventitious roots present. — Brunei: Temburong ... 7. *T. detritiferus*
5. Plants branched, adventitious roots absent. — Sabah 6

6. Leaves glabrous above..... 31b. *T. villosus* var. *borneensis*
6. Leaves pubescent above..... 31c. *T. villosus* var. *cordatus*

7. Plants branched; petals (both sexes) 2–2.5 mm long.....14. *T. longifolius*
7. Plants not branched; petals (both sexes) 8–9 mm long.....25. *T. sandakanensis*

8. Staminate flowers clustered into glomerules 9
8. 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.....
.....16. *T. lychnos*
10. Staminate flowers in several glomerules along the main rachis, pistillate inflorescences racemes.....31d. *T. villosus* var. *merrillianus*

11. Inflorescences large panicles ..... 8. *T. diffusus*
11. Inflorescences racemes or thyrses.....12

12. Leaf blade less than 1.5 cm wide .....10. *T. filiformis*
12. Leaf blade more than 1.5 cm wide .....31b. *T. villosus* var. *borneensis*

Key to the species of the Philippines

1. Petioles shorter than 3.5 cm.....2
1. Petioles longer than 3.5 cm 10

2. Venation triplinerved (basal veins distinct from others), lateral veins often fewer than 9 pairs.....3
2. Venation penninerved (basal veins identical to others), lateral veins often more than 9 pairs.....4

3. Leaves and petiole totally glabrous .....13. *T. laevigatus*
3. Leaves slightly hairy beneath, petiole hairy.....32a. *T. viridissimus* var. *viridissimus*

4. Leaves densely pubescent above ..... 19. *T. merrillii*
4. Leaves densely glabrous or glabrescent when young above.....5

5. Leaf blades: length more than 12 times width .....10. *T. filiformis*
5. Leaf blades: length (often far) less than 12 times width 6

6. Inflorescences (often far) more than 7 cm long .....14. *T. longifolius*
6. Inflorescences less than 7 cm long.....7

7. Staminate inflorescences paniculate or paintbrush-like thyrses (with at least secondary branches).....8
7. Staminate inflorescences racemes or racemose thyrses 9

8. Leaves paler above (when dry); staminate inflorescences glomerules .20. *T. oblongifolius*
8. Leaves paler beneath (when dry); staminate inflorescences paintbrush-like thyrses .....
..... 23. *T. polyanthus*

9. Pistillate sepals much accrescent when fruiting ..... 30. *T. victoriae*
9. Pistillate sepals not accrescent when fruiting .....31b. *T. villosus* var. *borneensis*

10. Inflorescences large panicles ..... 22. *T. philippinensis*
10. Inflorescences short cymes clustered on a rachis 11

11. Staminate flowers never cauliflorous; stamens 5 ..... 15. *T. longipes*
11. Staminate flowers often partly cauliflorous; stamens 3.....31d. *T. villosus* var. *merrillianus*

Key to the species of The Lesser Sunda Islands

1. Petiole and leaf blade completely glabrous; inflorescences thyrses, less than 4 cm long .. ..13a. *T. laevigatus* var. *laevigatus*
1. Petiole hairy, leaves hairy beneath; inflorescences panicles, more than 4 cm long .... 32. *T. viridissimus*

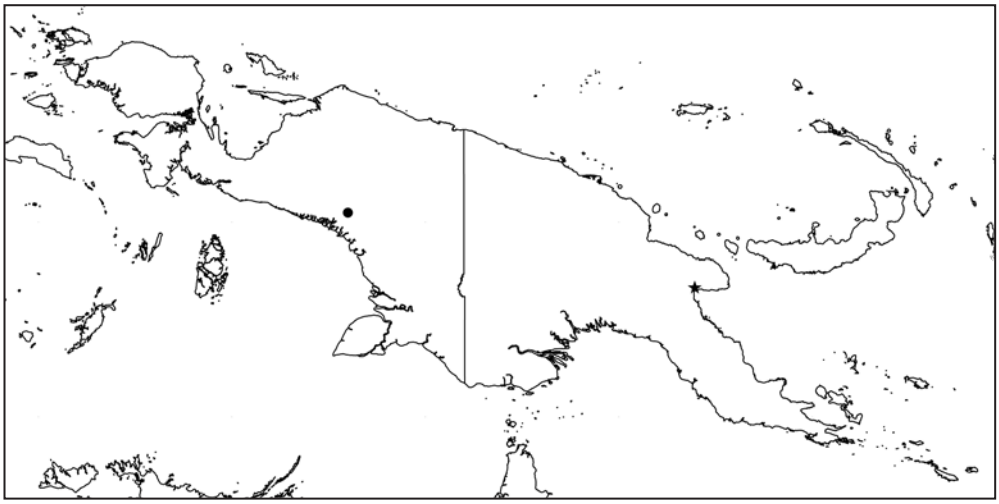
Key to the species of New Guinea

1. Stamens 3..... 1. *T. apetalogyne*
1. Stamens 5..... 12. *T. hartleyi*

1. ***Trigonostemon apetalogyne*** Airy Shaw — Map 2

Trigonostemon apetalogyne Airy Shaw, Kew Bull. 33 (1979) 534; Kew Bull., Addit. Ser. 8 (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,



Map 2 Distribution of *Trigonostemon apetalogyne* Airy Shaw (●) and *T. hartleyi* Airy Shaw (★).

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, filament free part 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), 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 caducous 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 the 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*).

2. ***Trigonostemon aurantiacus*** (Kurz ex Teijsm. & Binn.) Boerl. — Figure 3; Map 3

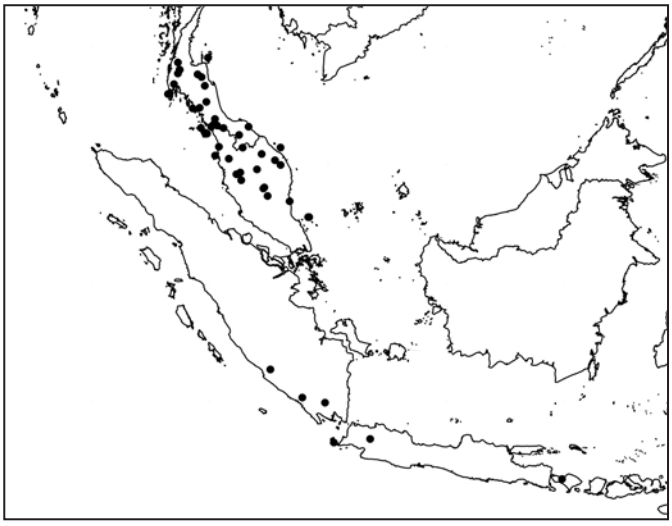
Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 284; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 93; in Engl. & Harms, Pflanzenfam. ed. 2, 19c (1931) 170; Jabl., Brittonia 15 (1963) 164, in obs.; Airy Shaw, Kew Bull. 23 (1969) 126; Kew Bull. 26 (1972a) 345, f. 11; Whitmore, Tree Fl. Malaya 2 (1973) 136; Airy Shaw, Hooker´s Icon. Pl. 38 (1974) tab. 3721; Kew Bull. 36 (1981) 352; Chantar. in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 576. — *Tylosepalum aurantiacum* Kurz ex Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 27 (1864) 50. — *Codiaeum aurantiacum* (Kurz ex Teijsm. & Binn.) Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1118. — Lectotype (designated here): *Teijsmann s.n.* (lecto L, barcode L.2260196), Indonesia, Java, cultivated in Bogor Botanical Garden (originally from Bangka?).

Actephila aurantiaca Ridl., Bull. Misc. Inform. Kew (1923) 360; Fl. Malay Penins. 3 (1924) 197. — Type: *Ridley s.n.*, Feb. 1917 (holo K, barcode K000959323), Malaya, Kelantan, Chaning Woods.

Actephilopsis malayana Ridl., Bull. Misc. Inform. Kew (1923) 361; Fl. Malay Penins. 3 (1924) 252; M.R.Hend., J. Malay Branch Roy. Asiat. Soc. 17 (1939) 68. — *Trigonostemon malayanus* (Ridl.) Airy Shaw, Kew Bull. 20 (1966) 413. — Syntypes: *Curtis 674* (K), Malaya, Penang, Ayer Hitam; *Haniff 1611* (?), Malaya, Perak, Gunung Kerbau; *Ridley 2300* (K), Malaya, Pahang, Kwala Tembeling.

Figure 3 *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl., cultivated in Bogor Botanical Garden (XV.J.A.XXXI.15, originally from Indochina), Java, Indonesia. a. Growing habit; b. leaves; c. short branch with cauliflorous flowers; d. staminate flowers; e. fruit. — Photos by Ren-Yong Yu.

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 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



Map 3 Distribution of *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl.

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.

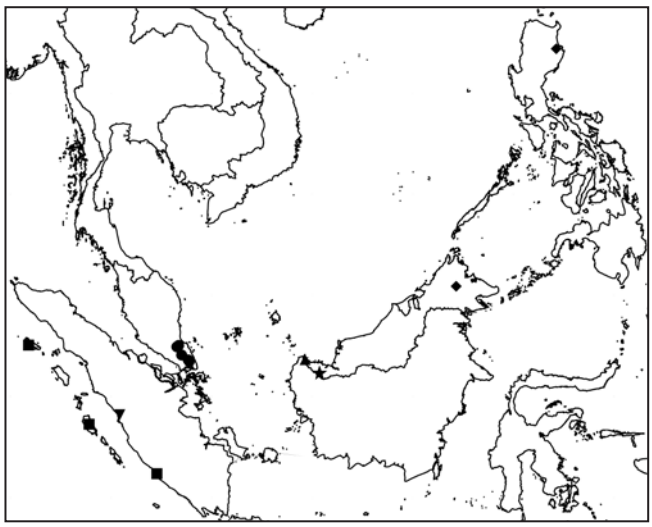
Habitat & Ecology — Lowland evergreen (often dipterocarp) forests, growing in understorey on limestone, along streams or on hill slopes. Altitude: 0–600 m. Flowering and fruiting: all year round.

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*.

3. ***Trigonostemon balgooyi*** R.Y.Yu & Welzen, *sp*. *nov*. — Figure 4; Map 4

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: *van Balgooy 7102* (holo L; iso K, KEP, SAN), Malaysia, Johor, Endau-Rompin, Kuala Jasin, 2°32'N, 103°22'E. 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.



Map 4 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. (◆).

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

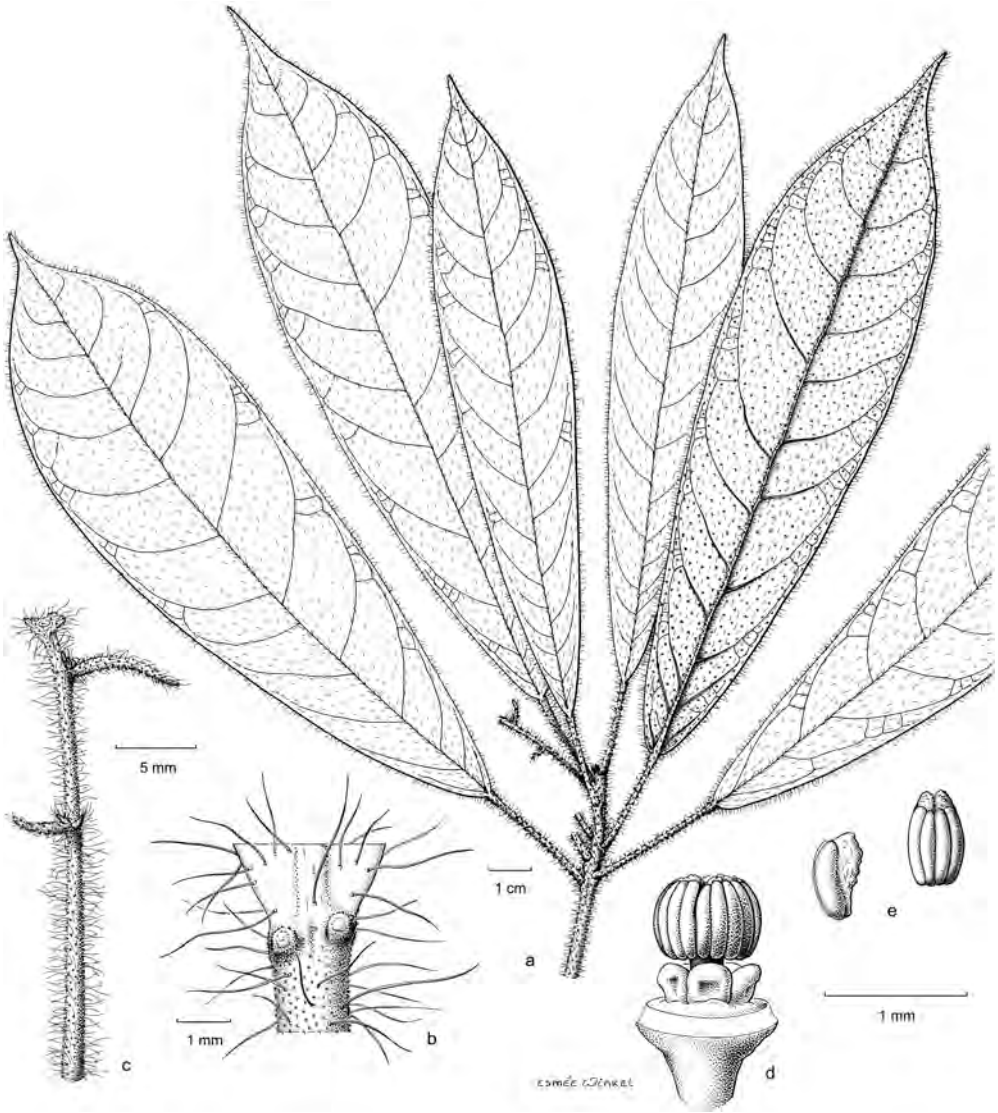


Figure 4 *Trigonostemon balgooyi* R.Y.Yu & Welzen. a. Flowering branch; b. leaf base with adaxial glands; c. part of inflorescence; d. staminate flower (sepals and petal removed); e. anthers, front and lateral views (all: *van Balgooy 7102*, L). — Drawing by Esmée Winkel, 2016.

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 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) rainforests on clay soil on hillsides 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. — Figure 5; Map 4

Trigonostemon beccarii Ridl., Bull. Misc. Inform. Kew (1925) 89; Jabl., Brittonia 15 (1963) 165; Airy Shaw, Kew Bull. 36 (1981) 353. — Type: *Beccari PS 965* (K, L), Sumatra, Padang, Sungei Buluh.

Trigonostemon longisepalus Ridl., Bull. Misc. Inform. Kew (1925) 89; Jabl., Brittonia 15 (1963) 165. — Type: *Brooks 8274* (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 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,

Figure 5 *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.

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*. *beccarii* 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*. *beccarii* and *T*. *longisepalus*.

5. ***Trigonostemon calcicolus*** (R.I.Milne) R.Y.Yu & Welzen, *comb*. *nov*. & *stat*. *nov*. — Map 4

Trigonostemon polyanthus Merr. var. *calcicolus* R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 30, in key, 33, f. 1. — Type: *Chew 679* (holo K; iso L), Sarawak, 1st Division, Kuching District, Tiang Bekap, Mt. Mentawa, 1°12'N, 110°23'E.

Small trees, 3 m tall; flowering branches c. 3 mm diam. *Outer bark* c. 0.1 mm thick, brownish, pubescent to hirsutulous 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, hirsutulous. *Leaves*: petiole 4.6–9 cm long, terete but grooved above, hirsutulous; 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 hirsutulous; midrib slightly raised and glabrous above, distinctly elevated and hirsutulous beneath, nerves 9–13 pairs, slightly raised and hirsutulous 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, hirsutulous; bracts to glomerules elliptic to lanceolate, 7–15 by 1.5–5 mm, apex acute to acuminate, hirsutulous outside, bracts to the flowers small, triangular to lanceolate, c. 0.3 by 0.1 mm, hirsutulous outside; pistillate inflorescences similar to staminate ones but with fewer flowers, 7–10 cm long, 0.7–1.1 mm diam, hirsutulous; bracts to the flowers lanceolate, c. 5 by 1.5 mm, hirsutulous outside. *Staminate flowers* (bud) 1.1–1.6 mm diam; pedicel 0.5–2 mm long, 0.3–0.5 mm diam (apex), thickened towards apex, densely hirsutulous; sepals elliptic, 0.5–1 by 0.3–0.5 mm, apex acute to rounded, hirsutulous 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 characters 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).

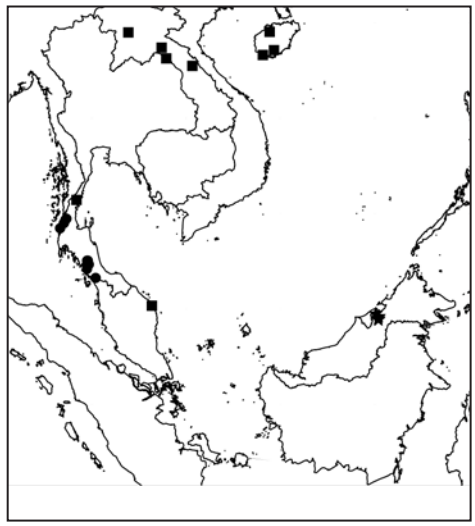
6. ***Trigonostemon capillipes*** (Hook.f.) Airy Shaw — Map 5

Trigonostemon capillipes (Hook.f.) Airy Shaw, Kew Bull. 20 (1967) 413; Kew Bull. 26 (1972a) 345; Whitmore, Tree Fl. Malaya 2 (1973) 135; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 202; R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 29, in key, 45; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 24; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 576. — *Dimorphocalyx capillipes* Hook.f., Fl. Brit. India 5 (1887) 404; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 33; Ridl., Fl. Malay Penins. 3 (1924) 266. — Type: *Lobb s.n.* (K, barcode K000894763), Singapore.

Trigonostemon pachyphyllus Airy Shaw, Kew Bull. 25 (1971) 546; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 27; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 581. — Type: *Kerr 19429* (holo K), Thailand, Chanthaburi, Khao Soi Dao.

Trigonostemon sp. nov., aff. *indicus* (Baill.) Müll.Arg.: Jabl., Brittonia 15 (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,



Map 5 Distribution of *Trigonostemon capillipes* (Hook.f.) Airy Shaw (●); *T. detritiferus* R.I.Milne (★); *T. flavidus* Gagnep. (■).

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 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 rainforests to mangrove forests. 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 recognised 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 — Figure 6; Map 5

Trigonostemon detritiferus R.I.Milne, Kew Bull. 49 (1994) 446, f. 2; Kew Bull. 50 (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, main branch 5–12 mm diam, without side 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;

Figure 6 *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 sap; 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.

Figure 6 (cont.)

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 forests, 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.

8. ***Trigonostemon diffusus*** Merr. — Map 4

Trigonostemon diffusus Merr., Sarawak Mus. J. 3 (1928) 525; Jabl., Brittonia 15 (1963) 164; R.I.Milne, Kew Bull. 50 (1995a) 27, in key, 29, in key, 46. — Type: *Mjöberg 145* (BM, K, UC*), Sarawak, Mt. 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* (bud) 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* R.I.Milne, should be synonymised under *T*. *polyanthus*, see note 3 under *T*. *polyanthus*.

9. ***Trigonostemon dipteranthus*** Airy Shaw — Map 4

Trigonostemon dipteranthus Airy Shaw, Kew Bull. 20 (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, 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 characterised 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 4

Trigonostemon filiformis Quisumb., Philipp. J. Sci. 41 (1930) 328, f. 7. — Type: *Clemens 16751* (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 (bud)–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 5

Trigonostemon flavidus Gagnep., Bull. Soc. Bot. France 69 (1922) 749; in Lecomte, Fl. Indo-Chine 5 (1925b) 320; P.T.Li & M.G.Gilbert in C.Y.Wu, P.H.Raven & D.Y.Hong, Fl. China 11 (2008) 273. — Type: *Harmand 3273* (P), Laos, in Lakhon mountains, near Me-Kong.

Trigonostemon heterophyllus Merr., Lingnan Sci. J. 9 (1930) 38; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 163; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 24; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (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 forests to deciduous hardwood or bamboo forests, 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 2

Trigonostemon hartleyi Airy Shaw, Kew Bull. 33 (1979) 535; Kew Bull., Addit. Ser. 8 (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 nearly entire 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, few-flowered; 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 — Rainforests, 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. — Figure 7; Map 6

Trigonostemon laevigatus Müll.Arg., Flora 47 (1864b) 538; in A.DC., Prodr. 15, 2 (1866) 1111; Boerl., Handl. Fl. Ned. Ind. 1 (1900) 232, 284; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 94; Merr., J. Straits Branch Roy. Asiat. Soc., Spec. No. (1921) 345 (2nd mentioning, first = *Microdesmis casearifolia* Planch., see Jablonski 1963: 168); Ridl., Fl. Malay Penins. 3 (1924) 265; Jabl., Brittonia 15 (1963) 167; Airy Shaw, Kew Bull. 26 (1972a) 346; Whitmore, Tree Fl. Malaya 2 (1973) 135; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 203; Kew Bull. 32 (1978) 417; Kew Bull. 36 (1981) 355; Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 25; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 578, f. 93. — Lectotype (designated here): *Motley 686* (lecto K), Borneo, Bangarmassing. Other syntype: *Barter s.n*. (K, barcodes K000959289, K000959290), Borneo.

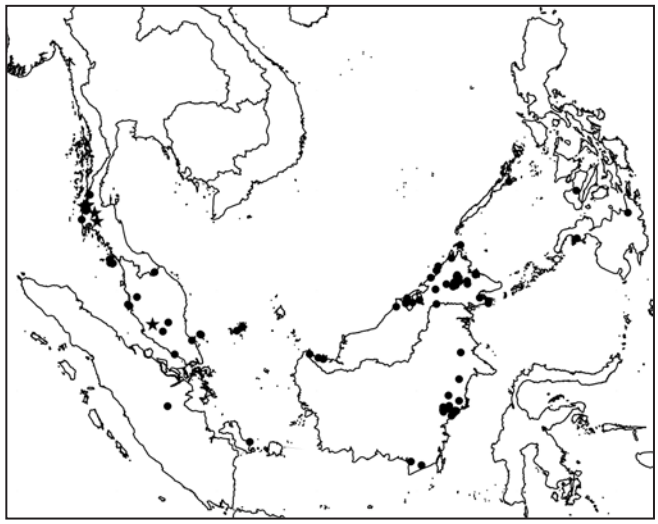
Trigonostemon everettii Merr., Philipp. J. Sci. 7, Bot. (1912) 408; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 408; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 451; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 46. — Type: *FB* (*Everett*) *7257* (A), Philippines, Negros, Mt. Silay.

Trigonostemon anomalus Merr., Philipp. J. Sci. 16 (1920) 569; Enum. Philipp. Fl. Pl. 2 (1923) 451. — Type: *FB* (*Villamil*) *22018* (A, US), Philippines, Mindanao, Zamboanga District, Naganaga.

Trigonostemon laevigatus Müll.Arg. var. *petiolaris* Airy Shaw, Kew Bull. 32 (1978) 417; R.I.Milne, Kew Bull. 50 (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., Brittonia 15 (1963) 168. — Voucher: *KEP* (*Strugnell*) *20275* (K, KEP, SING), Malaya, Pahang, Ulu Gali Raub. See note.

Trigonostemon sp. nov., aff. *chinensis* Merr.: Jabl., Brittonia 15 (1963) 168. — Voucher: *van Steenis 910* (BO, L, SING), Sumatra, Anambas Islands, Siantan Island, E of Terimpa. See note.



Map 6 Distribution of *Trigonostemon laevigatus* Müll.Arg. var. *laevigatus* (●) and *T. laevigatus* var. *croceus* (B.C.Stone) R.Y.Yu & Welzen (★).

Figure 7 *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 sap; 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.

Note — The species is wide-spread and is often recognised 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*** — Figure 7; Map 6

Sepals without a gland outside.

Distribution — As the species.

Habitat & Ecology — Mixed lowland dipterocarp forests, 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 variation 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 6

Trigonostemon croceus B.C.Stone, Malaysian Forester 43 (1980) 289. — Type: *Stone 9586* (holo KLU; iso K, L, PH*), Malaysia, Selangor, on the Pahang border at Genting Sempah.

Sepals with a gland outside.

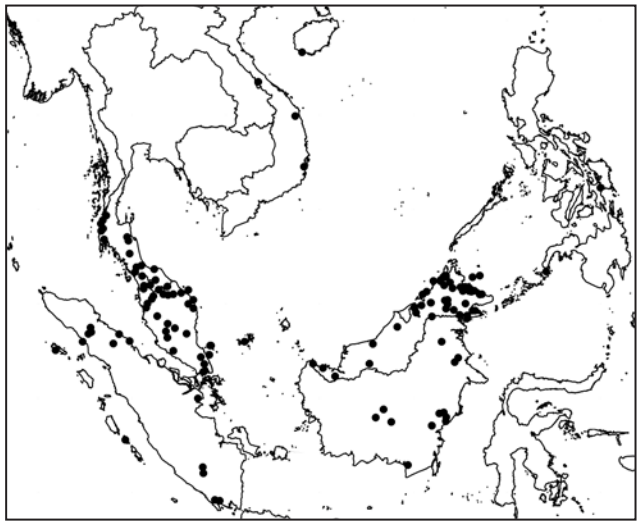
Distribution — Thailand, Malay Peninsula.

Habitat & Ecology — Hill evergreen forests 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*.

14. ***Trigonostemon longifolius*** Wall. ex Baill. — Figure 8; Map 7

Trigonostemon longifolius Wall. ex Baill., Étude Gén. Euphorb. (1858) 341; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1108; Kurz, For. Fl. Burma 2 (1877b) 406 ('*longifolium*'); Hook.f., Fl. Brit. India 5 (1887) 396; Pax & K.Hoffm. in Engl., Pflanzenfam. IV.147.iii (1911) 88, f. 28; Ridl., Fl. Malay Penins. 3 (1924) 264; Jabl., Brittonia 15 (1963) 162; Airy Shaw, Kew Bull. 26 (1972a) 347; Whitmore, Tree Fl. Malaya 2 (1973) 136; Airy Shaw, Kew Bull. 36 (1981) 355; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 26; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 579, f. 94. — [*Croton longifolius* Wall., Numer. List (1847) nr. 7717,



Map 7 Distribution of *Trigonostemon longifolius* Wall. ex Baill.

nom. nud., non Müll.Arg., Fl. Bras. 11(1873) 170]. — Lectotype (designated here): *Wallich 7717* (lecto K, barcode K000959328; isolecto BR, G, GH, K, barcode K000959327), Malaya, Penang Island. Other syntypes: *Griffith KD 4797* (K), Malaya, Malacca; *Griffith KD 4798* (K, U), India, Tenasserim and Andamans.

?*Athroisma dentatum* Griff., Notul. 4 (1854a) 478 ('*dentatis*'); Ic. Pl. Asiat. 4 (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., Notul. 4 (1854a) 477 ('*serratis*'); Ic. Pl. Asiat. 4 (1854b) pl. 585, f. 9. — Type: *Griffith s.n.*? (K?), Mergue, Tenasserim (see Airy Shaw 1972a: 347).

Croton longipedunculatus Elmer, Leafl. Philipp. Bot. 1 (1908) 311. — *Trigonostemon longipedunculatus* (Elmer) Elmer, Leafl. Philipp. Bot. 4 (1911) 1306; Pax & K.Hoffm. in Engl.,

Figure 8 *Trigonostemon longifolius* Wall. ex Baill., 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. young fruits. — Photos by Ren-Yong Yu.

Pflanzenr. IV.147.vii (1914) 408; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; R.I.Milne, Kew Bull. 50 (1995a) 38. — Type: *Elmer 7264* (A, BO, E, G, K), Philippines, Leyte, Prov. of Leyte, Palo.

Trigonostemon oblanceolatus C.B.Rob., Philipp. J. Sci. 6, Bot. (1911) 337; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 407; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47. — Type: *Williams 2185* (K, NY, US), Philippines, Mindanao, Zamboanga District, Sax River.

Prosartema gaudichaudii Gagnep., Bull. Soc. Bot. France 72 (1925a) 468, non *Trigonostemon gaudichaudii* (Baill.) Müll.Arg. Linnaea 34 (1865) 213. — *Trigonostemon gagnepainianus* Airy Shaw, Kew Bull. 32 (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., Univ. Calif. Publ. Bot. (1929) 162; Jabl., Brittonia 15 (1963) 162; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 202; R.I.Milne, Kew Bull. 50 (1995a) 27, in key, 29, in key, 41. — Type: *Elmer 20936* (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, Sunyatsenia 2 (1935) 262; H.S.Kiu, Fl. Republ. Popul. Sin. 44(2) (1996) 163. — Type: *F.C. How 70940* (A*, IBSC*, K, NY*, US*), China, Hainan.

Trigonostemon ionthocarpus Airy Shaw, Kew Bull. 21 (1968) 407; Kew Bull., Addit. Ser. 4 (1975) 203; R.I.Milne, Kew Bull. 50 (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, Kew Bull. 49 (1994) 445, f. 1; Kew Bull. 50 (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, Kew Bull. 50 (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., Bull. Misc. Inform. Kew (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, 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* unisexual 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.

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.

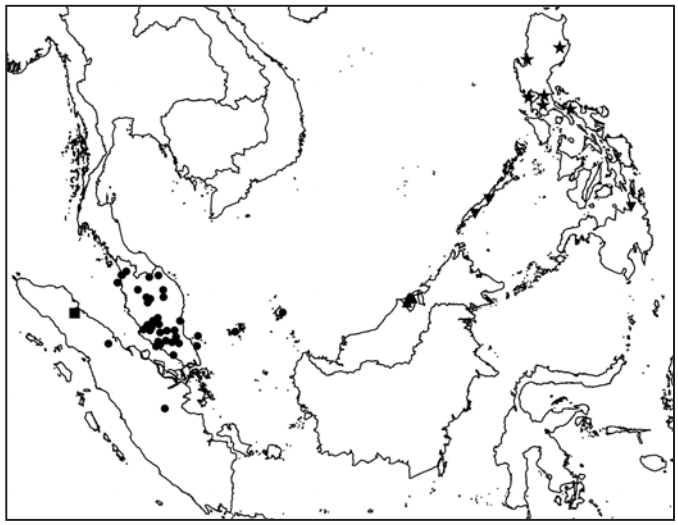
15. ***Trigonostemon longipes*** (Merr.) Merr. — Figure 9; Map 8

Trigonostemon longipes (Merr.) Merr., Philipp. J. Sci. 11, Bot. (1916b) 191; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xiv (1919) 41; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47. — *Dimorphocalyx longipes* Merr., Philipp. J. Sci. 1, Suppl. (1906) 82. — Lectotype (designated here): *FB* (*Whitford*) *1066* (lecto K; isolecto P), Philippines, Luzon, Bataan Prov., Mt. Mariveles. Other syntypes: *FB* (*Borden*) *1801* (BM, BO, K), Philippines, Luzon, Bataan Prov., Mt. Mariveles; *FB* (*Merrill*) *2699* (BM, K), Philippines, Luzon, Province of Rizal, Bosoboso.

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 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;

Figure 9 *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.



Map 8 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 (▼).

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 forests, on clay loam. Altitude: 175–250 m. Flowering: January to April, September; fruiting: January, April.

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.

16. ***Trigonostemon lychnos*** (R.I.Milne) R.Y.Yu & Welzen, *comb. nov. & stat. nov.* — Map 8

Trigonostemon polyanthus Merr. var. *lychnos* R.I.Milne, Kew Bull. 50 (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* (bud): pedicel covered by bracts, not seen; 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 forests; heath forests on sandy soil (Milne 1995a). Altitude: 50 m. Flowering: April.

Vernacular — Brunei : Sagubang Kayu.

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 8

Trigonostemon magnificus R.I.Milne, Kew Bull. 50 (1995b) 51, f. 1 ('*magnificum*'). — Type: *de Wilde & 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 semi-orbicular, 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 *de Wilde & de Wilde-Duyfjes 19280*, characterised by the tomentose indumentum, large and spreading inflorescences and sepals hairy on the inside.

18. ***Trigonostemon malaccanus*** Müll.Arg. — Figure 10; Map 8

Trigonostemon malaccanus Müll.Arg., Flora 47 (1864a) 482; in A.DC., Prodr. 15, 2 (1866) 1110; Hook.f., Fl. Brit. India 5 (1887) 396; Pax & K.Hoffm. in Engl., Pflanzenfam. IV.147.iii (1911) 90; Ridl., Fl. Malay Penins. 3 (1924) 265; Jabl., Brittonia 15 (1963) 154; Whitmore, Fl. Malay Penins. 2 (1973) 136; Airy Shaw, Kew Bull. 36 (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 hirsutulous, 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 the length. *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.

Distribution — Thailand, Malay Peninsula, Sumatra.

Habitat & Ecology — Evergreen forests to recently logged-over 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.

Figure 10 *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.

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 8

Trigonostemon merrillii Elmer, Leafl. Philipp. Bot. 4 (1911) 1304; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 407; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; R.I.Milne, Kew Bull. 50 (1995a) 27, in key, 29, in key, 44. — Type: *Elmer 12819* (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*: petiole 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 glomerules along the main rachis, peduncle slender, 8–9 cm long and 0.4–0.7 mm diam, sericeous, with a few depauperate glomerules 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* not seen. *Fruits* c. 1.25 cm diam, glabrous; sepals not much accrescent. *Seeds* streaked or conspicuously mottled.

Distribution — Philippines (endemic).

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

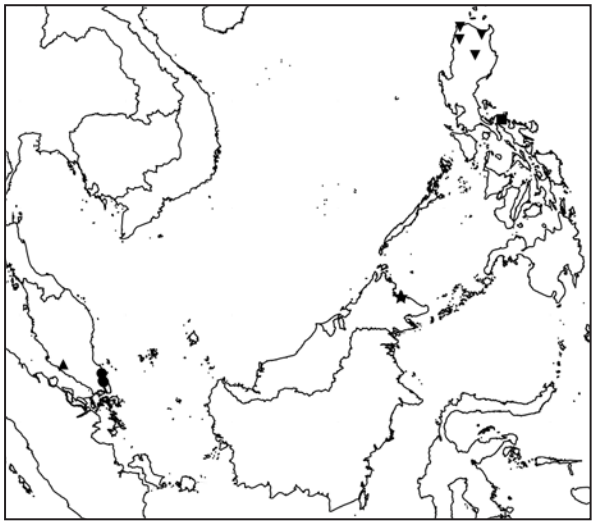
Note — The species resembles *T*. *oblongifolius* in the male inflorescences but differs from the latter by the blade being hairy on both sides. The description of the fruits is based on Elmer (1911).

20. ***Trigonostemon oblongifolius*** Merr. — Map 9

Trigonostemon oblongifolius Merr., Philipp. J. Sci. 7, Bot. (1912) 409; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 407; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47. — Type: *BS* (*Ramos*) *13965* (A, US), Philippines, Luzon, Prov. Cagayan, Abulug River.

Trigonostemon luzoniensis Merr., Philipp. J. Sci. 16 (1920) 568; Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47. — Type: *PNH* (*Ramos & Edaño*) *33539* (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* (bud) 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;



Map 9 Distribution of *Trigonostemon oblongifolius* Merr. (▼); *T. pentandrus* Pax & K.Hoffm. (▲); *T. polyanthus* Merr. (■); *T. rufescens* Jabl. (●); *T. sandakanensis* Jabl. (★).

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.

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. — Figures 11, 12; Map 9

Trigonostemon pentandrus Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 406; Jabl., Brittonia 15 (1963) 164. — Type: *Hubert Winkler 1792* (not traced), Malaysia, Negeri Sembilan, Gunung Angsi near Sungei Gadub. Neotype (designated here): *KEP FRI* (*R.Y. Yu*) *86653* (neo L; isoneo 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 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 bifid into 2 arms of 1.2–1.5 mm length, thickened at apex. *Fruits* c. 5.5 mm diam, 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.

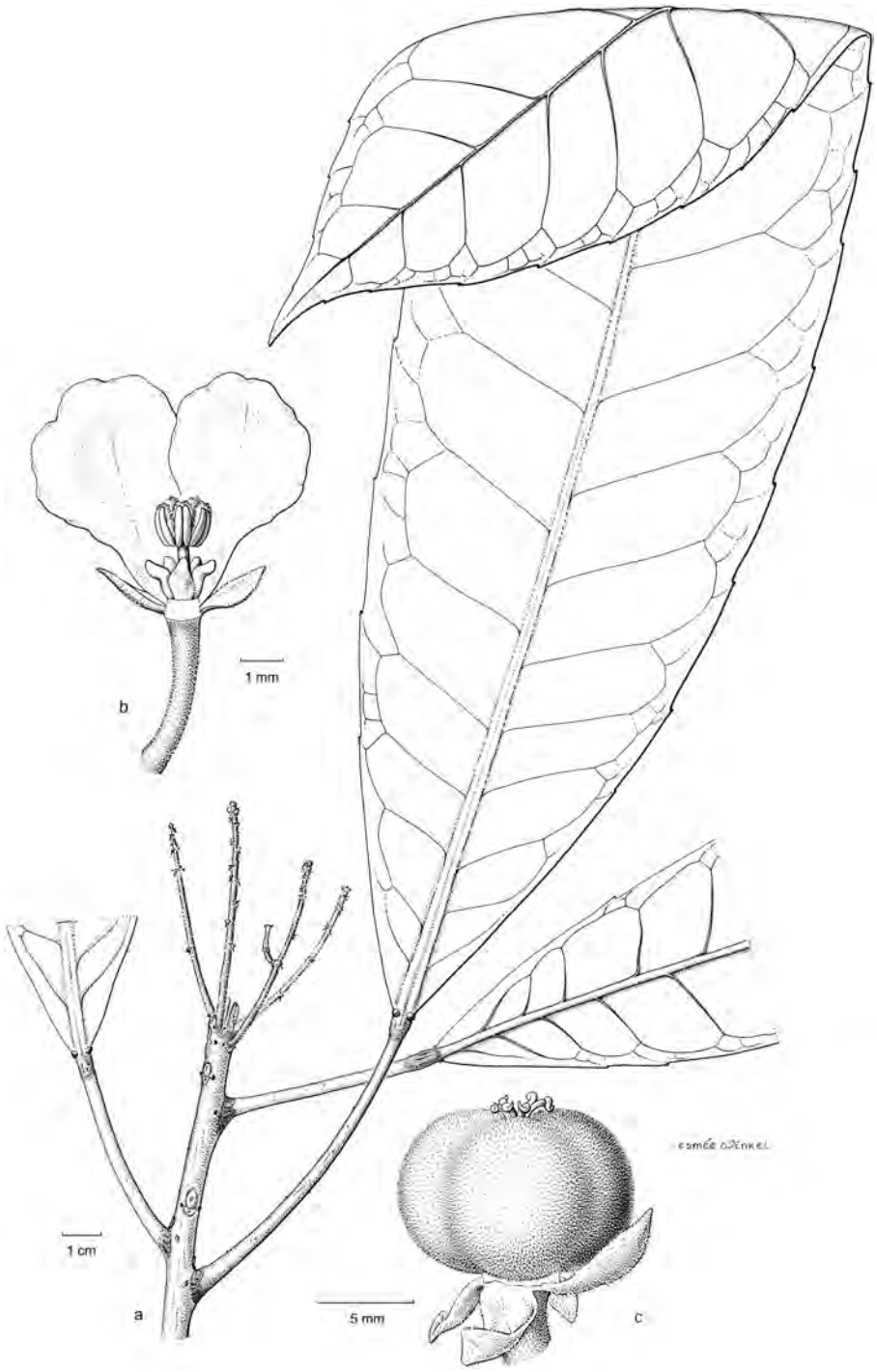


Figure 11 *Trigonostemon pentandrus* Pax & K.Hoffm. a. Flowering branch; b. staminate flower (3 sepals and 3 petals removed); c. fruits (all: *Franck 1372*, C). — Drawing by Esmée Winkel, 2016.

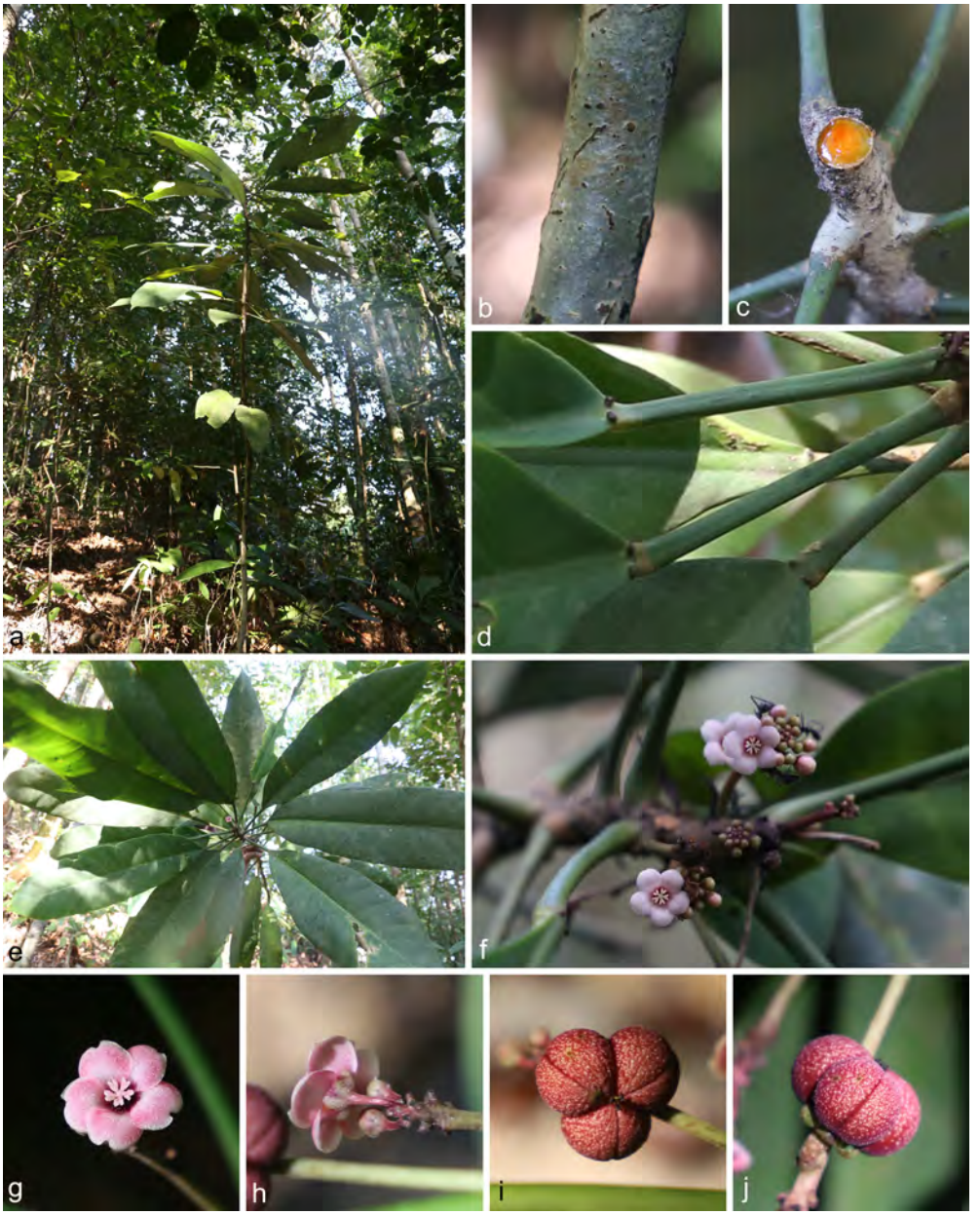


Figure 12 *Trigonostemon pentandrus* Pax & K.Hoffm., from Gunung Angsi, Negri Sembilan, Malay Peninsula. a. Growing habit; b. bark; c. orange sap; d. leaf base with adaxial glands; e. top view of the tree; f. inflorescences, ants are potential pollinators; g, h. staminate flowers; i, j. fruit. — Photos by Ren-Yong Yu.

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.

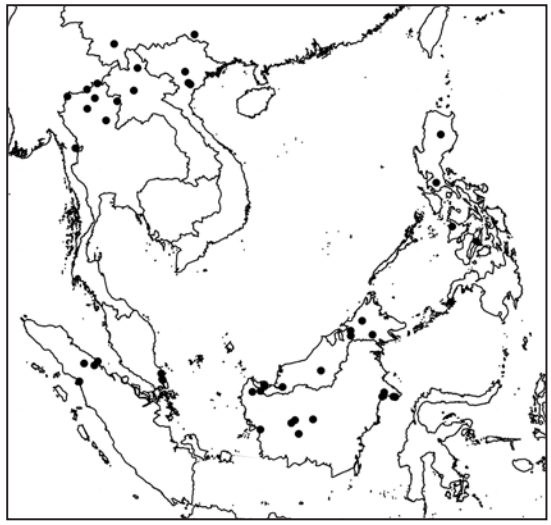
22. ***Trigonostemon philippinensis*** Stapf — Figure 13; Map 10

Trigonostemon philippinensis Stapf, Leafl. Philipp. Bot. 1 (1907) 206 ('*philippinense*'); Pax & K.Hoffm. in Engl., Pflanzenfam. IV.147.iii (1911) 91; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Kew Bull. 36 (1981) 355; Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; R.I.Milne, Kew Bull. 50 (1995a) 27, in key, 29, in key. — Type: *Elmer 8326* (BO, G*, K, L), Philippines, Luzon, Laguna Prov., Los Baños.

Trigonostemon thyrsoideus Stapf, Bull. Misc. Inform. Kew (1909) 264 ('*thyrsoideum*'); Airy Shaw, Kew Bull. 26 (1972a) 348; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 166; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 29; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 584, pl 32: 1; P.T.Li & M.G.Gilbert. in C.Y.Wu, P.H.Raven & D.Y.Hong, Fl. China 11 (2008) 274. — Type: *Henry 11947* (A*, K, NY*), China, Yunnan, Simao (Szemao).

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

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); sap 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



Map 10 Distribution of *Trigonostemon philippinensis* Stapf.

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.

Figure 13 *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.

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, 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. *Infructescences* 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 9

Trigonostemon polyanthus Merr., Philipp. J. Sci. 9, Bot. (1914) 492; Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 48. — Type: *BS* (*Ramos*) *1645* (BM, BO, BRI*, G*, GH*, L, NY*, P*, SING), Philippines, Samar, Cauayan Valley.

Trigonostemon diffusus Merr. subsp. *condensus* R.I.Milne, Kew Bull. 50 (1995a) 47. — Type: *PNH* (*Lagrimas et al*.) *39433* (holo K; iso L), 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, single- 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. *Pistillate 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.

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 of *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. For example, 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. — Figure 14; Map 9

Trigonostemon rufescens Jabl., Brittonia 15 (1963) 152, f. 2; Whitmore, Tree Fl. Malaya 2 (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

Figure 14 *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 sap; f. staminate flower; g. fruit. — Photos by Ren-Yong Yu.

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. — Figure 15; Map 9

Trigonostemon sandakanensis Jabl., Brittonia 15 (1963) 159, f. 5, 6; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 204; R.I.Milne, Kew Bull. 50 (1995a) 27, in key, 30, in key. — Type: *SAN* (*Wood*) *16018* (holo SING; iso BO, BRI*, K, KEP, L, SAN), 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

Figure 15 *Trigonostemon sandakanensis* Jabl., from Kabili-Sepilok Forest Reserve, Sandakan, Sabah, Malaysia. a. Growing habit; b. adventitious root on the main branch; c. red sap. — Photos by Ren-Yong Yu.

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).

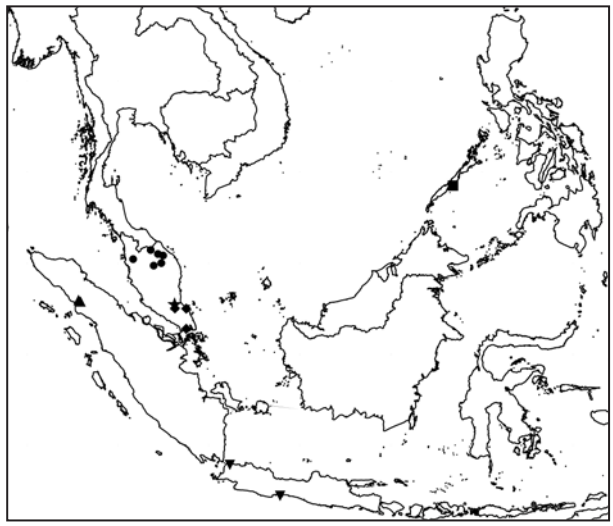
Habitat & Ecology — Primary forests, near stream. Altitude: 5–20 m. Flowering: April to June; fruiting: December.

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

26. ***Trigonostemon scopulatus*** R.Y.Yu & Welzen, *sp*. *nov*. — Figure 16; Map 11

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* (*Cockburn*) *7859* (holo L; iso K, KEP, SING), Malaysia, Johore, Ulu Endau, Labis FR, Compt. 277. Paratypes: *KEP FRI* (*Ng*) *5207* (KEP, L), Malaysia, Johore, Mersing, Arong FR, Compt. 90; *Lai* & *Ali Ibrahim LJ 22* (SING), Singapore, Mandai Forest, next to Mandai Columbarium; *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



Map 11 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 (▲).

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

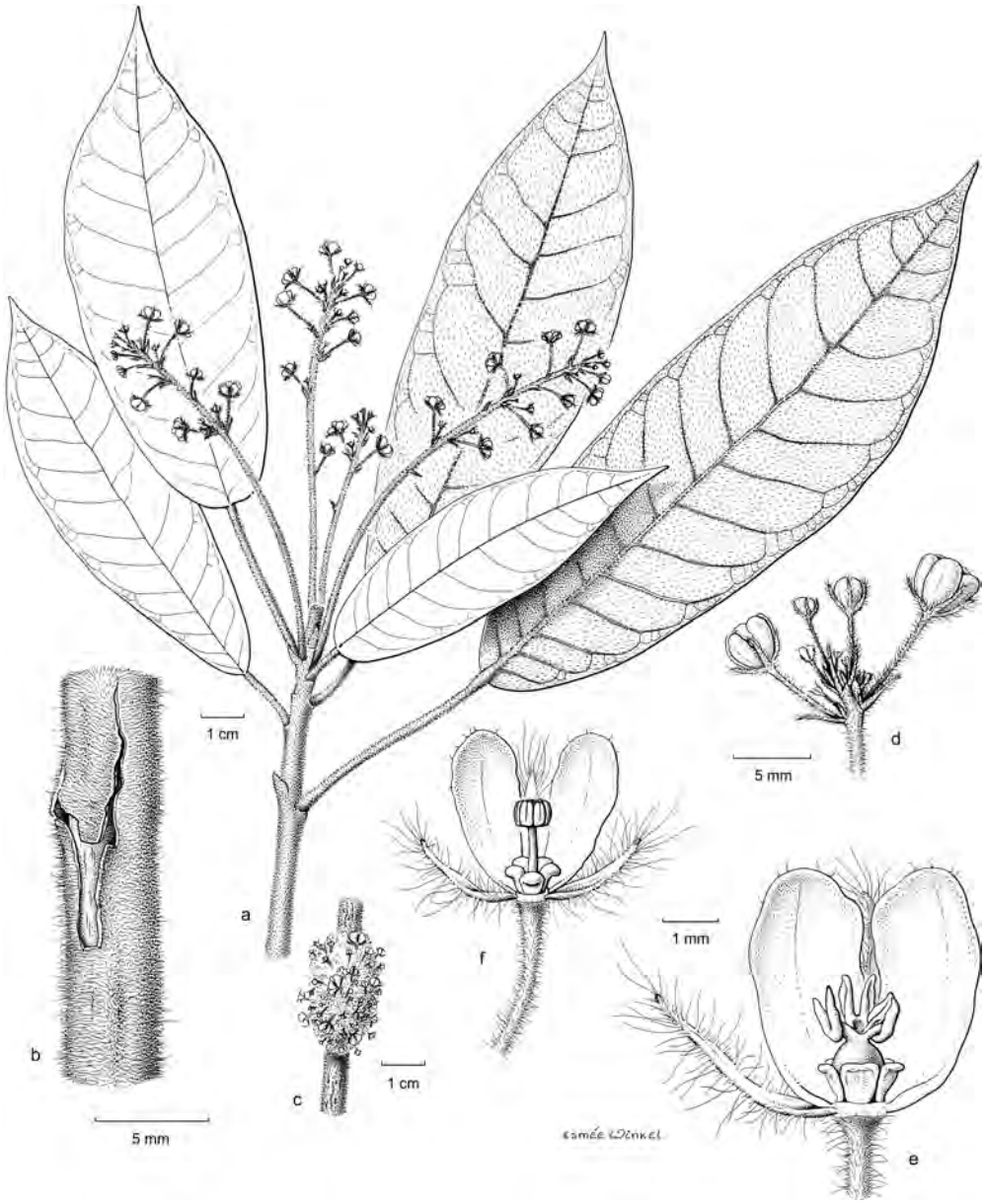


Figure 16 *Trigonostemon scopulatus* R.Y.Yu & Welzen. a. Flowering branch; b. bark; c. cauliflorous inflorescence; d. apex of inflorescence; e. pistillate flower (3 sepals and 3 petals removed); f. staminate flower (2 sepals and 3 petals removed) (all: *KEP FRI* (*P.F. Cockburn*) *7859*, L). — Drawing by Esmée Winkel, 2016.

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 forests near logging roads; moist gullies. Altitude: low. Flowering: March.

27. ***Trigonostemon serratus*** Blume — Map 11

Trigonostemon serratus Blume, Bijdr. (1825) 600 (‘*serratum*’); Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1110; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 92; Backer & Bakh.f., Fl. Java 1 (1963) 495; Airy Shaw, Kew Bull. 37 (1982) 36. — Lectotype (designated here): *Blume 1648* (lecto 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.

Distribution — Java (endemic).

Habitat & Ecology — Rainforests. 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 11

Trigonostemon sinclairii Jabl., Brittonia 15 (1963) 154, f. 3, 4; Whitmore, Tree Fl. Malaya 2 (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 papillose-ciliate, 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, papillate-hispid (only one layer, not villose), veinlets reticulate, obscure above. *Inflorescences*: staminate ones axillary, racemose 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 forests to newly logged forests on hillsides. Flowering: May and August; fruiting: July and September.

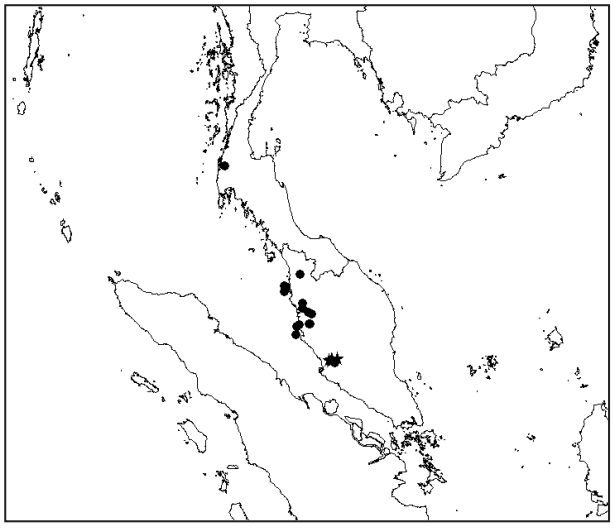
Note — An extremely hairy species with large accrescent pistillate sepals.

29. ***Trigonostemon verticillatus*** (Jack) Pax — Map 12

Trigonostemon verticillatus (Jack) Pax in Engl., Planzenfam. IV.147.iii (1911) 87; Jabl., Brittonia 15 (1963) 164; Airy Shaw, Kew Bull. 26 (1972a) 349; Whitmore, Tree Fl. Malaya 2 (1973) 136; Chantar.,Thai Forest Bull. (Bot.) 33 (2005) 30; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 585, pl. 31: 2. — *Enchidium verticillatum* Jack, Malayan Misc. 2, 7 (1822) 90; Comp. Bot. Mag. 1 (1835) 257, excl. synon. Rumphius; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1256; Merr., J. Arnold Arbor. 33 (1952) 224. — Neotype (designated here): *Maingay KD 1403* (neo L; isoneo BM, K), Malay Peninsula, Malacca (see note).

Telogyne indica Baill., Étude Euphorb. (1858) 328, pl. 11, f. 13. — *Trigonostemon indicus* (Baill.) Müll.Arg., Linnaea 34 (1865) 214; in A.DC., Prodr. 15, 2 (1866) 1107; Hook.f., Fl. Brit. India 5 (1887) 398; Ridl., Fl. Malay Penins. 3 (1924) 264; Jabl., Brittonia 15 (1963) 152. — Lectotype (designated here): *Wallich 7997* (lecto 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 (bud); 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,



Map 12 Distribution of *Trigonostemon verticillatus* (Jack) Pax. var. *verticillatus* (●) and *T. verticillatus* var. *salicifolius* (Ridl.) Whitmore (★).

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 monotypic 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 12

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 12

Trigonostemon verticillatus (Jack) Pax var. *salicifolius* (Ridl.) Whitmore, Gard. Bull. Singapore 26 (1972) 52; Fl. Malay Penins. 2 (1973) 136. — *Trigonostemon salicifolius* Ridl., Bull. Misc. Inform. Kew (1923) 366; Fl. Malay Penins. 3 (1924) 264; Jabl., Brittonia 15 (1963) 152, f. 1; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 204. — Type: *Ridley s.n*. (holo K), Malaysia, Selangor, Kanching.

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*. — Figure 17; Map 11

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, Panacan, Aborlan, Victoria Mountains.

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* (bud) 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.

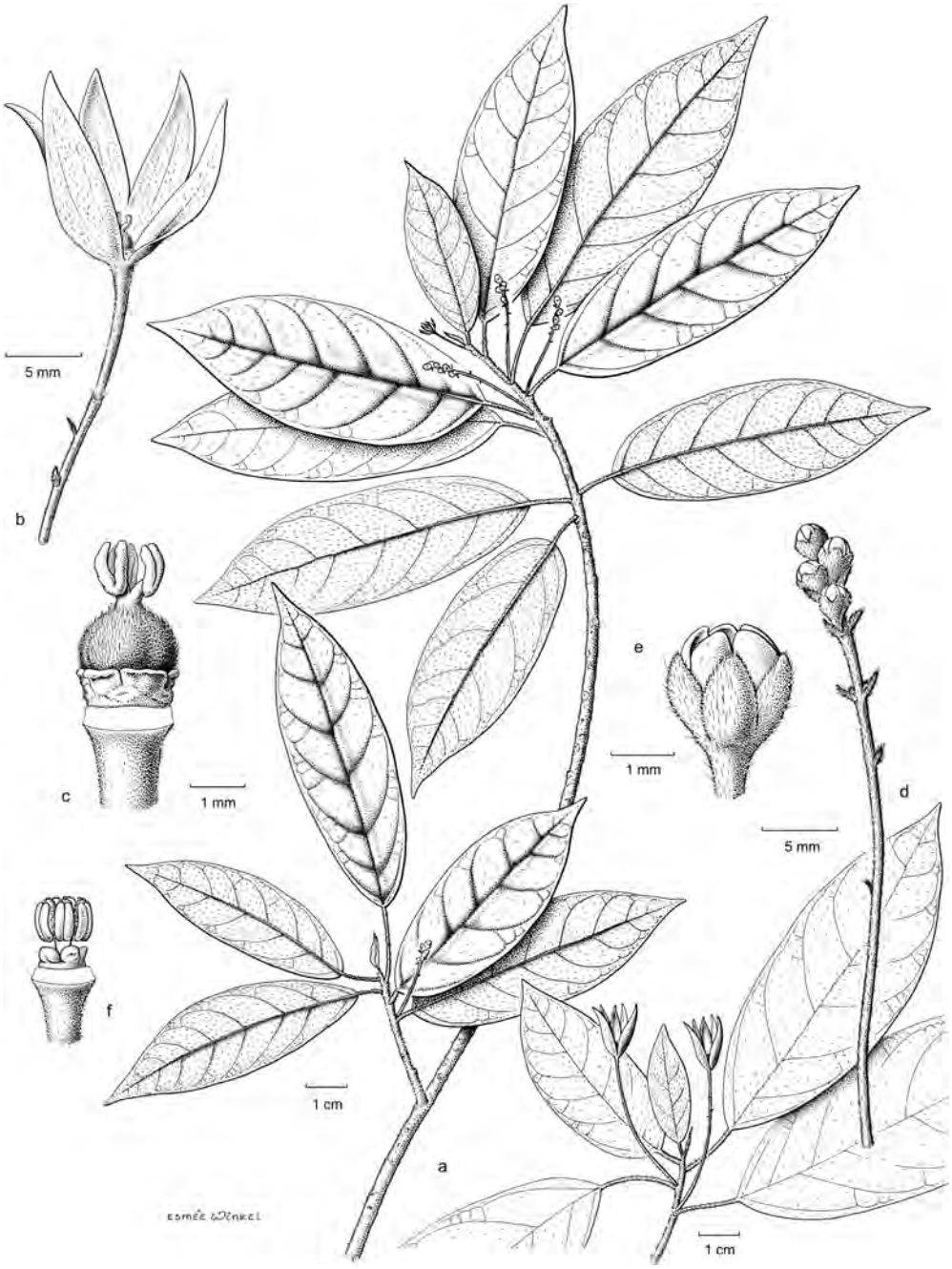


Figure 17 *Trigonostemon victoriae* R.Y.Yu & Welzen. a. Two flowering branches; b. pistillate inflorescences; c. pistillate flower (sepals and petals removed); d. staminate inflorescence; e. staminate flower, showing the sepals and petals; f. staminate flower (sepals and petals removed) (all: *PNH* (*Sulit*) *12317*, L). — Drawing by Esmée Winkel, 2016.

31. ***Trigonostemon villosus*** Hook.f. — Figures 18, 19, 20; Maps 13, 14

Trigonostemon villosus Hook.f., Fl. Brit. India 5 (1887) 397; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 88; Ridl., Fl. Malay Penins. 3 (1924) 265; Jabl., Brittonia 15 (1963) 158; Whitmore, Tree Fl. Malaya 2 (1973) 135; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 204; Kew Bull. 36 (1981) 358; R.I.Milne, Kew Bull. 50 (1995a) 37. — Type: *King's collector s.n*. (K), Malaya, Perak.

Trigonostemon tomentellus Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 89. — Type: *Anonymous s.n*. (not traced), Malacca.

Trigonostemon carnosulus Airy Shaw, Kew Bull. 32 (1978) 415. — Type: *CF* (*Yeop*) *844* (holo K), Malaya.

Trigonostemon polyanthus auct. non Hook.f.: R.I.Milne, Kew Bull. 50 (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, 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 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.

Figure 18 *Trigonostemon villosus* Hook.f. var. *villosus* (a, c, f), from Forest Research Institute Malaysia, Kepong, Malay Peninsula and *Trigonostemon villosus* Hook.f. var. *borneensis* (Merr.) Airy Shaw (b, d, e, g–m), from Segaliud Lokan Forest Reserve, Sabah, Malaysia. a, b. Growing habit; c, d. top view of the tree; e. bark and reddish sap; f, g. pistillate inflorescence; h, i. staminate flower; j, k. pistillate flower; l, m. fruit. — Photos by Ren-Yong Yu.

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 (Maps 13, 14) of great morphological variation. We made this treatment based on a large number of collections showing that this massive variation actually connects all single forms together into a species complex, even though the extreme forms often do not resemble each other (see Figure 20). These extremes, furthermore, have often become the source of synonyms, where the species

Figure 18 (cont.)

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 Figure 20 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

Figure 19 *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.

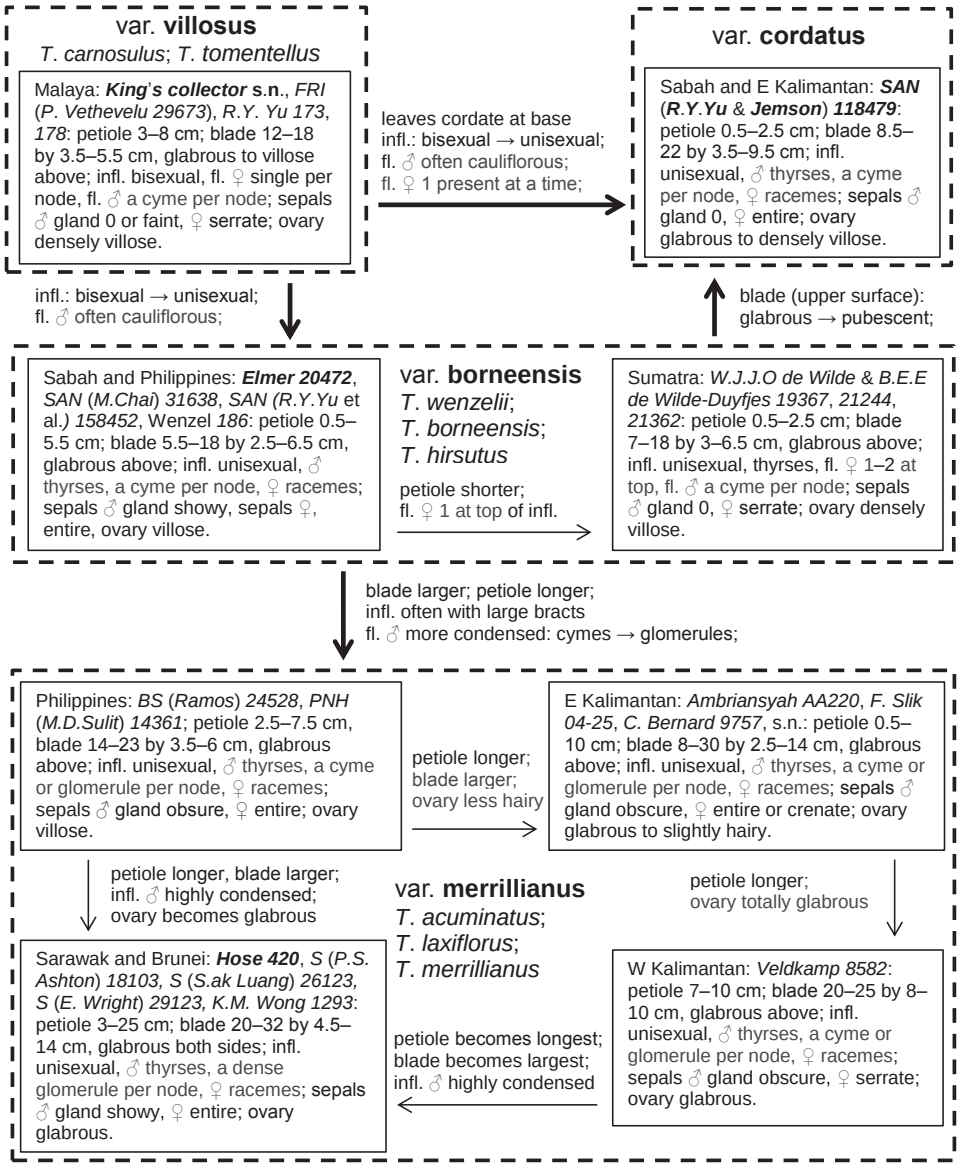


Figure 20 Continuous morphological variation of *T. villosus*. Frames in dashed lines refer to the varieties, the accepted name of each variety is in **bold** with synonyms shown below it; frames in solid lines refer to intermediate forms among the variation with example specimens; arrows between the 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***.

petiole sizes (Figure 20), 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.

Key to the varieties

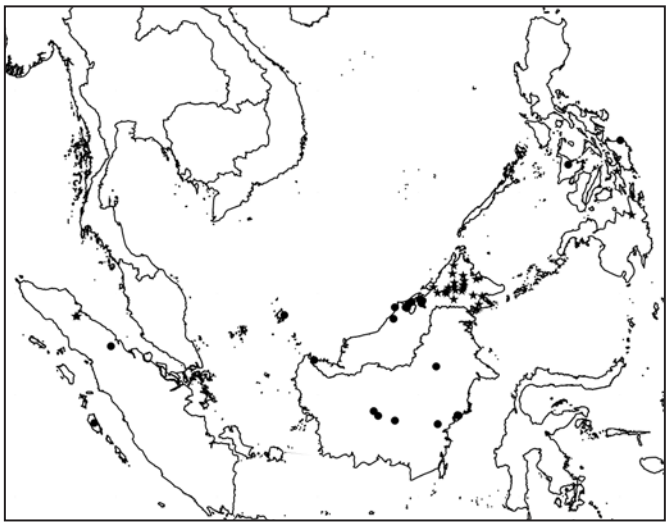
1. Petiole longer than 8 cm ..... d. var. *merrillianus*
1. Petiole shorter than 8 cm 2

2. Inflorescences bisexual. — Malay Peninsula ..... a. var. *villosus*
2. Inflorescences unisexual. — Sumatra, Sabah, Philippines 3

3. Leaves glabrous above. — Sumatra, Sabah, Philippines ..... b. var. *borneensis*
3. Leaves pubescent above. — Sabah ..... c. var. *cordatus*

a. var. ***villosus*** — Figure 18a, c, f; Map 14

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 not seen. *Pistillate flowers*:



Map 13 Distribution of *Trigonostemon villosus* Hook.f. var. *borneensis* (Merr.) Airy Shaw (★) and *T. villosus* var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen (●).

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 hillsides 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 — Figure 18b, d, e, g–m; Map 13

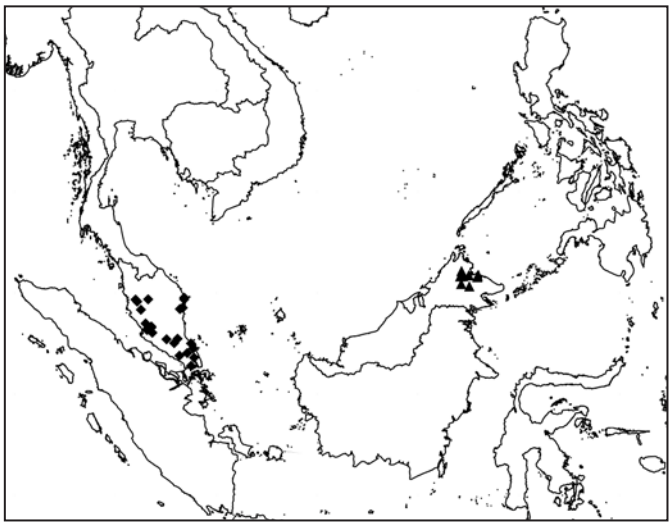
Trigonostemon villosus Hook.f. var. *borneensis* (Merr.) Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 205. — *Trigonostemon borneensis* Merr., Univ. Calif. Publ. Bot. 15 (1929) 162; Jabl., Brittonia 15 (1963) 162; Whitmore, Tree Fl. Malaya 2 (1973) 136. — Type: *Elmer 20742* (A, BISH*, BM, BR*, CAS*, CM*, G*, GH*, HBG*, K, L, M*, MICH*, NY*, P*, PH*, S*, SING, U, UC*), Borneo, near Tawao.

Trigonostemon hirsutus C.B.Rob., Philipp. J. Sci. 6, Bot. (1911) 335; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 406; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 451; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 30, in key, 41, f. 3. — Type: *BS* (*Robinson*) *11798* (not seen), Philippines, Mindanao, Zamboanga District, Port Banga (synonymy somewhat doubtful as the type is lost).

Trigonostemon wenzelii Merr., Philipp. J. Sci. 8, Bot. (1913) 380; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xiv (1919) 41; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 453. — Type: *Wenzel 186* (A*, G*, GH*, L, US*), Philippines, Leyte, Dagami.

Trigonostemon villosus Hook.f. var. *caesius* R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 30, in key, 37. — Type: *SAN* (*Ampuria*) *40236* (holo K; iso SAN), Sabah, Beaufort District, Beaufort Hill.

Leaves: petiole 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



Map 14 Distribution of *Trigonostemon villosus* Hook.f. var. *villosus* (◆) and *T. villosus* var. *cordatus* R.Y.Yu & Welzen (▲).

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 allegiance 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.* — Figure 19; Map 14

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* (*Yu et al.*) *158458* (L, SAN), Sabah, Tepid, Tawai Forest Reserve; *SAN* (*Yu et al.*) *158459* (L, SAN), Sabah, Tepid, Tawai Forest Reserve; *SAN* (*Yu et al.*) *158460* (L, SAN), Sabah, Tepid, Tawai Forest Reserve; *SAN* (*Yu & Jemson*) *158480* (L, SAN), Sabah, Sandakan, Kabili-Sepilok Forest Reserve; *SAN* (*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 13

Trigonostemon merrillianus Airy Shaw, Kew Bull. 25 (1971) 549, non *T. borneensis* Merr., Univ. Calif. Publ. Bot. 15 (1929) 162; Kew Bull., Addit. Ser. 4 (1975) 203. — *Dimorphocalyx* (?) *borneensis* Merr., Philipp. J. Sci. 11, C. Bot. (1916a) 73. — Type: *Hose 420* (holo K; iso L), Sarawak, 4th Division, Baram District, Entoyut River.

Trigonostemon acuminatus Merr., Philipp. J. Sci. 11, Bot. (1916b) 190; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xiv (1919) 41; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 451; Airy Shaw, Alphab.

Enum. Euphorb. Philipp. Isl. (1983b) 46. — Type: *BS* (*Ramos*) *24528* (A, BM, BO, K, L, US), Philippines, Samar, Catubig River.

Trigonostemon laxiflorus Merr., Philipp. J. Sci. 16 (1920) 567; Enum. Philipp. Fl. Pl. 2 (1923) 451; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47. — Type: *BS* (*Ramos & Edaño*) *31097* (A*, K, P*, US*), Philippines.

Leaves: petiole 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 Figure 20. 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 15

Trigonostemon viridissimus (Kurz) Airy Shaw, Kew Bull. 25 (1971) 545; Whitmore, Tree Fl. Malaya 2 (1973) 135; Airy Shaw, Kew Bull., Addit. Ser. 5 (1975) 205; Kew Bull. 36 (1981) 358; Kew Bull. 37 (1982) 36; Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 48; R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 29, in key. — *Sabia viridissima* Kurz, J. Asiac. Soc. Bengal part 2, Nat. Hist., 41 (1872) 304; Hook.f., Fl. Brit. India 2 (1876) 3; Kurz, Forest Fl. Burma 1 (1877a) 301. — *Blachia viridissima* (Kurz) King, J. Asiac. Soc. Bengal 65 (1896) 455, in obs. — *Kurziodendron viridissimum* (Kurz) N.P.Balakr., Bull. Bot. Surv. India 8 (1966) 68, pl. 1, f. 1–7. — Type: *Kurz s.n.* (K, barcodes K000246871, K000246872), India, Andamans.

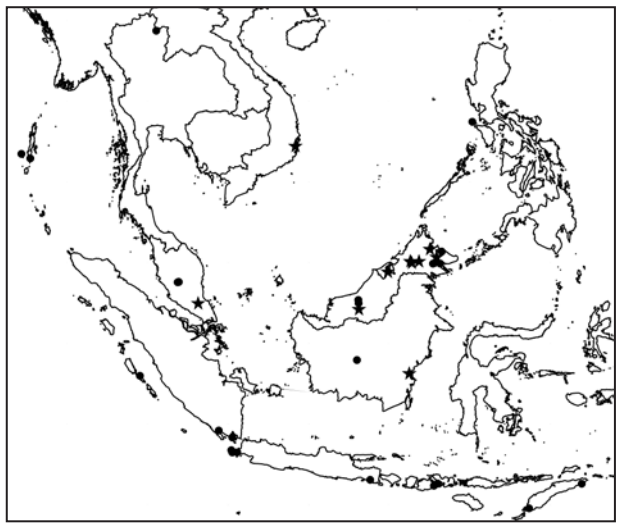
Trigonostemon ovatifolius J.J.Sm., Meded. Dep. Landb. 10 (1910) 583; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.v (1912b) 286; Backer & Bakh.f., Fl. Java 1 (1963) 495. — Type: *Koorders s.n.* (BO?, not seen), Java.

Trigonostemon membranaceus Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 91. — Type: *Koorders 32989* (BO), Java: Djapara.

Trigonostemon sumatranus Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 90; S.Moore, J. Bot. 63, Suppl. (1925) 100 (as synonym of *T. forbesii* Pax = *Wetria insignis* (Steud.) Airy Shaw); Merr., Papers Mich. Acad. Sci. 20 (1935) 101; Jabl., Brittonia 15 (1963) 163 (see note under *T. philippinensis*); W.L.Stern, Amer. J. Bot. 54 (1967) 671; Whitmore, Fl. Malay Penins. 2 (1973) 135. — Type: *Forbes 2647* (BM, K, L), Sumatra.

Trigonostemon macgregorii Merr., Philipp. J. Sci. 16 (1920) 566; Enum. Philipp. Fl. Pl. 2 (1923) 452. — Type: *BS* (*McGregor*) *32424* (K, P, US), Philippines, Panay, Antique Province, Culasi.
Neotrigonostemon diversifolius Pax & K.Hoffm., Notizbl. Bot. Gart. Berlin-Dahlem 10 (1928) 385; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (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, 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



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

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 *T. viridissimus*, which is the oldest and accepted name 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 15

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 15

Trigonostemon viridissimus (Kurz) Airy Shaw var. *elegantissimus* (Airy Shaw) Airy Shaw, Kew Bull., Addit. Ser. 5 (1975) 206. — *Trigonostemon elegantissimus* Airy Shaw, Kew Bull. 20 (1966) 48; Kew Bull. 32 (1978) 417; Whitmore, Tree Fl. Malaya 2 (1973) 135; R.I.Milne, Kew Bull. 50 (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., Bull. Soc. Bot. France 72 (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 recognised 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 of the differences between the two varieties although he treated them as two separate species.

33. ***Trigonostemon wetriifolius*** Airy Shaw & Ng — Figure 21; Map 11

Trigonostemon wetriifolius Airy Shaw & Ng, Malaysian Forester 41 (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* (bud): 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).

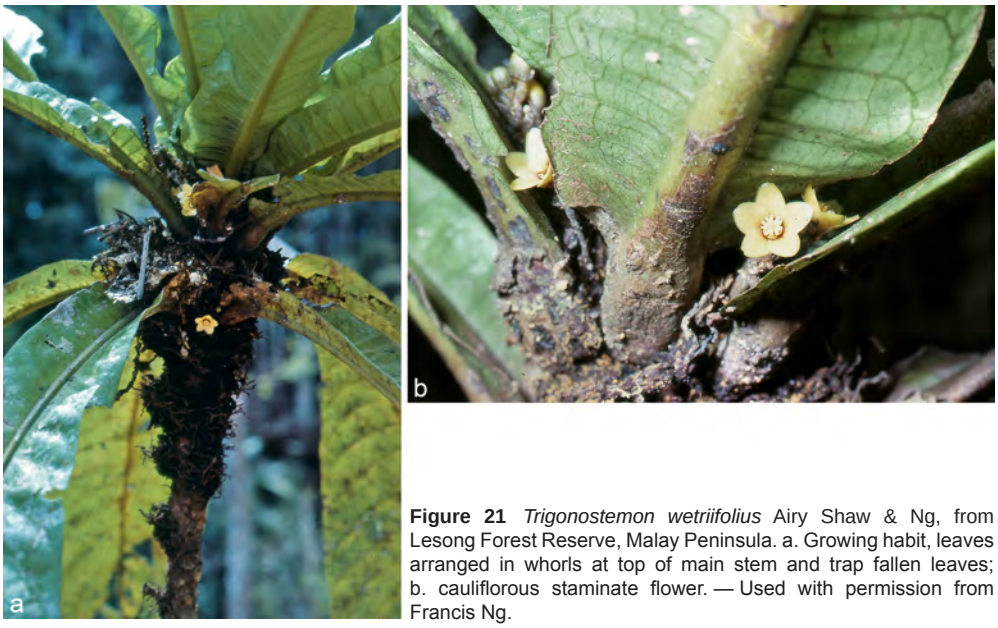


Figure 21 *Trigonostemon wetriifolius* Airy Shaw & Ng, from Lesong Forest Reserve, Malay Peninsula. a. Growing habit, leaves arranged in whorls at top of main stem and trap fallen leaves; b. cauliflorous staminate flower. — Used with permission from Francis Ng.

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

Note — Only known from the type specimen. Two slides of the plant (see Figure 21, taken by Francis Ng) are attached with the type specimen. Descriptions of the 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*. — Figure 22; Map 11

This species resembles *T. aurantiacus*, but differs by the sepals being covered by dense silky hairs and the 5 (in stead of 3) stamens. — Type: *de Wilde & 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, 2°55'N, 99°57'E. Paratype: *de Wilde & 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, 3°N, 97°50'E.

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 sericeous; 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, 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 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 forests on yellow-red loamy soil over basalt rocks. Altitude: 50–200 m. Flowering and fruiting: July.

Note — Only known from the two collections mentioned above.

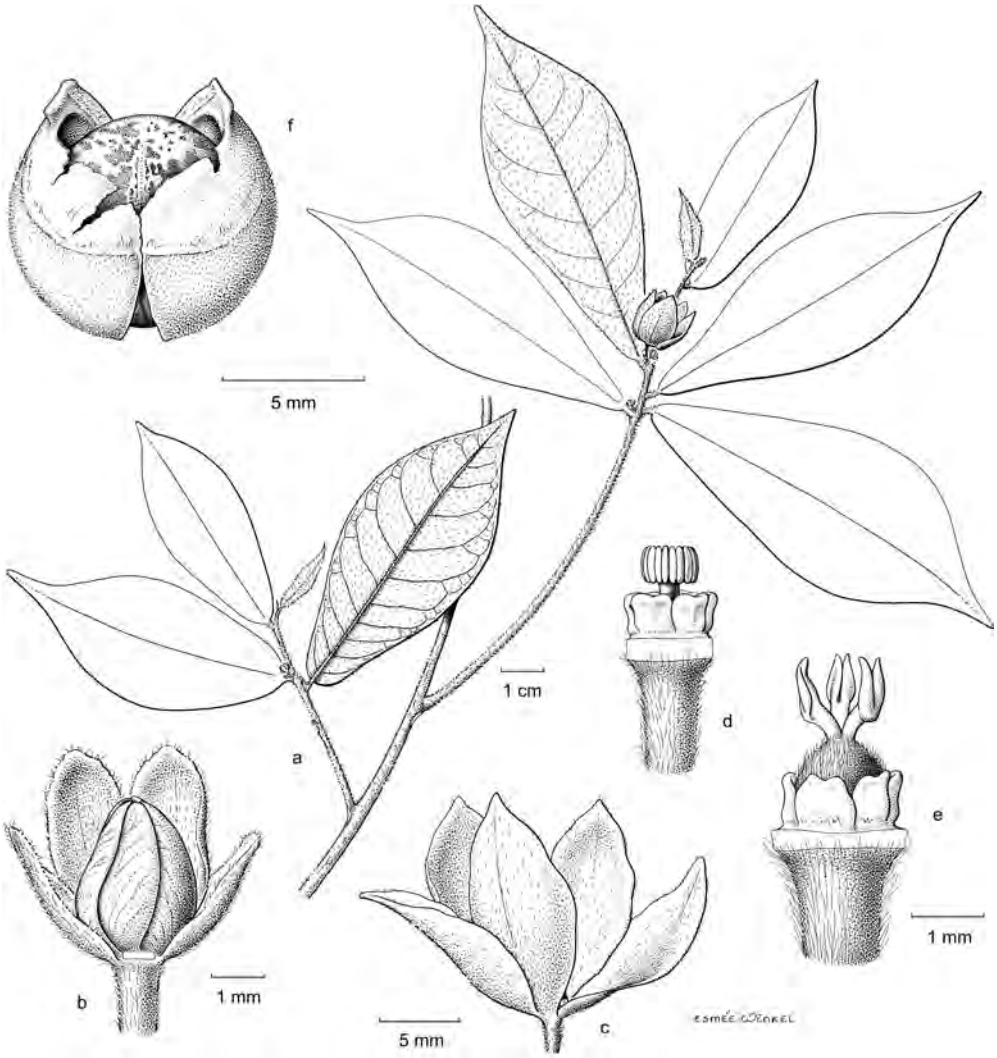


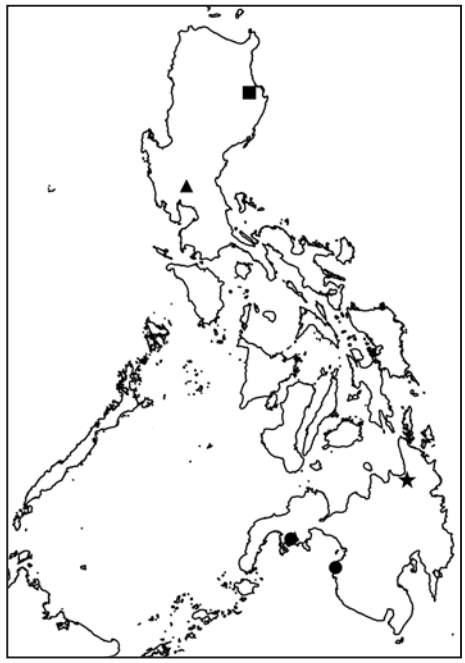
Figure 22 *Trigonostemon wildeorum* R.Y.Yu & Welzen. a. Flowering branch; b. staminate flower, showing the sepals and petals (one sepal removed); c. pistillate flower, showing the accrescent sepals; d. staminate flower (sepals and petals removed); e. pistillate flower; f. one dehiscing coccus with a marbled seed (all: *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 20274*, L). — Drawing by Esmée Winkel, 2016.

DOUBTFUL SPECIES

35. ***Trigonostemon angustifolius*** Merr. — Map 16

Trigonostemon angustifolius Merr., Philipp. J. Sci. 20 (1922a) 396. — Type: *BS* (*Ramos & Edaño*) *36764* (of *36560*) (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.



Map 16 Distributions of *Trigonostemon angustifolius* Merr. (●); *T. cumingii* Müll.Arg. (★); *T. stenophyllus* Quisumb. (■); *T. whiteanus* (Croizat) Airy Shaw (▲).

Distribution — Philippines (Mindanao, endemic).

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

Vernacular name — Pululi (Merrill 1922a).

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 (1922a). Knowledge of 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 16

Trigonostemon cumingii Müll.Arg., Linnaea 34 (1865) 213; in A.DC., Prodr. 15, 2 (1866) 1107. — *Tritaxis cumingii* (Müll.Arg.) Benth., J. Linn. Soc., Bot. 17 (1878) 221; Pax in Engl., Pflanzenr. IV.147.i (1910) 114; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 449. — *Dimorphocalyx cumingii* (Müll.Arg.) Airy Shaw, Kew Bull. 23 (1969) 124; Alphab. Enum. Euphorb. Philipp. Isl. (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 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 condensed. A molecular phylogenetic study is necessary to determine this species affiliation.

37. ***Trigonostemon stenophyllus*** Quisumb. — Map 16

Trigonostemon stenophyllus Quisumb., Philipp. J. Sci. 41 (1930) 330, f. 8. — Type: *BS* (*Ramos & Edaño*) *47331* (A, K, NY*, UC*), Philippines, Luzon, Isabela Prov., Mt. Moises.

Shrubs, up to 1 m tall; branches terete, 2–3.5 mm diam, pubescent when young, glabrous when mature. *Stipules* unknown. *Leaves*: petiole 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 specimens 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 16

Trigonostemon whiteanus (Croizat) Airy Shaw, Kew Bull. 38 (1983a) 68; Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 48. — *Cheilosa whiteana* Croizat, J. Arnold Arbor. 23 (1942b) 507; Airy Shaw, Kew Bull. 16 (1963) 365, in note. — Type: *FB* (*Curran*) *17733* (A, 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; venations 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 the 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., Kew Bull. (1928) 75. — Type: *KEP* (*Nur or Henderson*) *18595* (SING), Malay Peninsula, Pulau Tioman, Sedagong. = ***Omphalea malayana*** Merr. (Milne 1995a).

Trigonostemon asahanensis Croizat, J. Arnold Arbor. 23 (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, Leafl. Philipp. Bot. 10 (1939) 3735; Airy Shaw, Kew Bull. 20 (1966) 413. — *Dimorphocalyx bulusanensis* (Elmer) Airy Shaw, Kew Bull. 27 (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 Engl., Pflanzenr. IV.147.iii (1911) 88; S.Moore, J. Bot. 63, Suppl. (1925) 100; Jabl., Brittonia 15 (1963) 165. — Type: *Forbes 1892* (GH, L), Indonesia, Sumatra, Lampong, Mt. Tengamoes [= Gunung Tanggamus]. = ***Wetria insignis*** (Steud.) Airy Shaw (van Welzen 1998).

Trigonostemon macrophyllus (Müll.Arg.) Müll.Arg., Linnaea 34 (1865) 213. — *Tritraxis macrophylla* Müll.Arg., Flora 47(1864a) 482. — *Ostodes macrophylla* (Müll.Arg.) Benth. ex Pax & K.Hoffm. in Engl., Pflanzenr. IV.147. iii (1911) 18; Ridl., Fl. Malay Pen. 3 (1924) 269, f. 153. — Type: *Griffith KD 4788* (K), Malacca. = ***Paracroton pendulus*** (Hassk.) Miq. (Esser 2007).

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

Trigonostemon zeylanicus (Müll.Arg.) Müll.Arg., Linnaea 34 (1865) 213. — *Tritaxis zeylanicus* Müll.Arg., Flora 47 (1864a) 482. — 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 Baill.
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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Chapter 3 Taxonomic notes on *Trigonostemon* (Euphorbiaceae) in the Philippines

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Abstract Descriptions of five *Trigonostemon* species in the Philippines (four endemic) are updated with taxonomic notes based on herbarium collections and field observations. A new species of *Trigonostemon* is described. All species treated here are illustrated with photos. The formerly uncertain species, *T. stenophyllus*, is now synonymised with *T. filiformis*. In addition to *T. pentandrus*, three more *Trigonostemon* species are reported to cohabit with ants. A new identification key and an updated identification list of *Trigonostemon* species in the Philippines are provided.

Key words

Euphorbiaceae
Philippines
revision
taxonomy
Trigonostemon

INTRODUCTION

Trigonostemon Blume belongs to the Euphorbiaceae subfamily Crotonoideae (e.g., Webster 2014, Radcliffe-Smith 2001, Wurdack et al. 2005) and includes four sections (based on molecular data, Yu et al. 2019b). Fourteen species are present in the Philippines, of which eight are endemic and two are uncertain as based on this study. This monoecious genus is mainly recognised by the 5-merous unisexual flowers (without staminodes or pistillode), colourful (often purple or yellow) petals present in both staminate and pistillate flowers, and the 3 or 5 connate stamens.

The earliest 16 species of *Trigonostemon* were described for the flora of the Philippines (all considered endemic then) by Elmer (1911), Merrill (1912, 1913, 1914, 1916b, 1920, 1922a), Robinson (1911) and Stapf (1907) before 1923 when Merrill compiled all these names in his 'Enumeration of Philippine flowering plants'. Later, Quisumbing (1930) described *T. filiformis* and *T. stenophyllus* (both endemic, the latter was based on inadequate material). Airy Shaw (1983a, b) updated Merrill's checklist by synonymizing *T. anomalus* Merr. with *T. laevigatus* Müll.Arg. and regarding *T. whiteanus* (Croizat) Airy Shaw under *Trigonostemon* instead of *Cheilosa* Blume even though staminate flowers, the most distinctive for the genus, were lacking. Besides, Airy Shaw (1983b) overlooked Quisumbing's (1930) two species. Yu & van Welzen (2018) revised all *Trigonostemon* species in Malesia. In this revision, four *Trigonostemon* species (*T. angustifolius* Merr., *T. cumingii Müll.Arg*. [= *Tritaxis cumingii* (Müll.Arg.) Benth.; Bentham 1878, Yu et al. 2019b], *T. stenophyllus* Quisumb. and *T. whiteanus*) in the Philippines were considered uncertain due to inadequate material.

Among the four major distribution centres of *Trigonostemon* in Malesia, the Philippines has the most endemic species (the other three centres: Malay Peninsula: 6 endemic species; Sumatra 3; Borneo 3; Yu & Welzen 2018), but relatively few specimens have been collected in this area. Only 56 collections (15 species) from the Philippines were included in the last revision (Yu & van Welzen 2018), which is in marked contrast to the 299 collections from the Malay Peninsula (16 species), 81 collections from Sumatra (11 species) and 375 collections from Borneo (11 species). Moreover, herbarium collections often have an obvious limitation for a complete description of the plants, as only the young and immature leaves can fit on the specimen sheet whereas the mature ones (often much bigger) are ignored and generally only one sex or one generative phase (flower or fruit) is visible. Having visited the major Philippine herbaria (CAHUP, LBC, PNH, PUH, acronyms following Thiers et al., continuously updated, and the De La Salle University Herbarium [DLSUH]) and conducted field observations of the plants, we present this work to improve previous taxonomy treatments and to update the descriptions of the Philippine species of *Trigonostemon* with more accurate measurements. A newly found *Trigonostemon* species is also described here. In addition, more *Trigonostemon* species are found to cohabit with ants, just as *T. pentandrus* Pax & K.Hoffm. (an endemic species in Gunung Angsi, Malay Peninsula; Yu & Welzen 2018). The interactions between the plants and the ants are unknown. A possible mechanism is that the plants offer nectar, for instance via the basal leaf blade glands or the protruding appendage in the connective, in exchange for protection by the ants against herbivorous insects and overgrowing plants.

Key to the Species of the Philippines

(the numbered taxa are fully described below, for descriptions of the other taxa see Yu & van Welzen (2018); the two uncertain species, *T. angustifolius* Merr. and *T. whiteanus* (Croizat) Airy Shaw, are not included in the key)

1. Venation triplinerved (basal veins distinctly thicker than others); stigmas slightly or not bifid 2
1. Venation penninerved (basal veins identical to others); stigmas deeply bifid (to at least half length of stigma) 3

2. Leaves and petiole totally glabrous; inflorescences shorter than 4 cm .... *T. laevigatus* var. *laevigatus*
2. Leaves slightly hairy beneath, petiole hairy; inflorescences usually longer than 4 cm .... *T. viridissimus* var. *viridissimus*

3. Flowers yellow 4
3. Flowers dark reddish or purplish..... 5

4. Inflorescences racemes, up to 4.5 cm long ..... 4. *T. palustris*
4. Inflorescences panicles, (often much) more than 4.5 cm long ..... *T. philippinensis*

5. Petals abruptly narrowed at base (claw-like), disc (in both sexes) annular; fruits often warty 6
5. Petals gradually narrowed at base, disc divided into 5 lobes; fruits not warty..... 8

6. Inflorescences racemose; staminate flowers never cauliflorous, single per node .... *T. longifolius*
6. Inflorescences paniculate; staminate flowers cauliflorous and/or staminate flowers clustered in glomerules per node..... 7

7. Leaves densely pubescent on both sides..... 3. *T. merrillii*
7. Leaves glabrous above and sparsely pubescent beneath ..... *T. oblongifolius*

8. Leaves often with 2 pairs of adaxial glands at base; petals without a honey mark 9
8. Leaves often with 1 pair of adaxial glands at base; petals with a flame-like honey mark in the centre..... 10

9. Stamens 5..... 2. *T. longipes*
9. Stamens 3..... 5. *T. victoriae*

10. Staminate inflorescences paniculate thyrses, densely branched (broom-like or paintbrush-like) and main rachis not visible at the end of the inflorescences..... *T. polyanthus*
10. Staminate inflorescences racemose thyrses, not (much) branched, with a clear single main rachis still visible at the end of the inflorescences 11

11. Inflorescences often very slender, thinner than 0.6 mm diam; sepals in pistillate flower never accrescent .....1. *T. filiformis*
11. Inflorescences thicker than 0.8 mm diam; sepals in pistillate flower sometimes accrescent (in *T. villosus* var. *merrillianus*) 12

12. A few (often fewer than 10) staminate flowers in cymes per node; pistillate sepals not accrescent in fruit, always smaller than petals .....*T. villosus* var. *borneensis*
12. Many (often more than 20) staminate flowers in glomerules per node; pistillate sepals often accrescent in fruit, then larger than petals.....6. *T. villosus* var. *merrillianus*

TAXONOMY

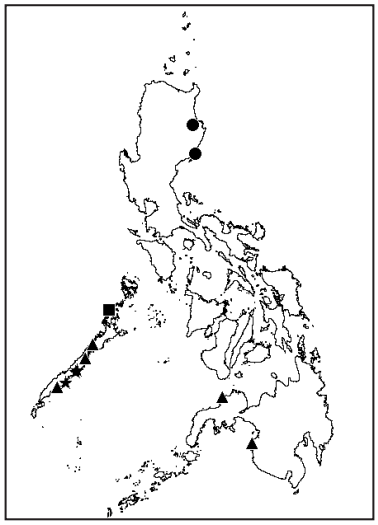
Throughout this part, an asterisk refers to a specimen seen as image. The sections, as defined by Yu et al. (2019b), are indicated for all species: sect. *Trigonostemon*, sect. *Pycnanthera* Benth., sect. *Spinipollen* R.Y.Yu & Welzen, and sect. *Tylosepalum* (Kurz) Benth. Full descriptions are provided for the new species and the taxa for which additional information was found; for the generic description and descriptions of the other taxa, see Yu & Welzen (2018).

1. ***Trigonostemon filiformis*** Quisumb. — sect. ***Trigonostemon*** — Figure 23; Map 17

Trigonostemon filiformis Quisumb., Philipp. J. Sci. 41 (1930) 328, f. 7; R.Y.Yu & Welzen, Blumea 62 (2018) 194. — Lectotype (designated here): *Clemens 16751* (lecto NY*; isolecto A, UC*), Philippines, Luzon, Isabela Prov., Mt. Moises.

Trigonostemon stenophyllus Quisumb., Philipp. J. Sci. 41 (1930) 330, f. 8; R.Y.Yu & Welzen, Blumea 62 (2018) 225. — Type: *BS* (*Ramos & Edaño*) *47331* (A, K, NY*, UC*), Philippines, Luzon, Isabela Prov., Mt. Moises.

Shrubs, up to 1 m tall; branches terete, 2.2–3.5 mm diam, pubescent when young, glabrescent. *Outer bark* 0.1–0.2 mm thick, brown when young, grey when old, glabrous; inner bark 0.1–0.4 mm thick, dark brown, sap red, low quantity; wood pale yellow to brown. *Stipules* subulate, 0.5–0.8 mm long, pubescent, caducous. *Leaves*: petiole terete, 1–6.5 cm long, 1–2.8 mm diam, sometimes grooved above, slightly pubescent when young; blade oblong to lanceolate (to almost linear), 8–26.5 by 1–4.5 cm, coriaceous, base acute to rounded, 2 adaxial glands present, margin slightly distantly serrate, teeth falcate to subulate, apex acuminate, both sides reddish brown and pubescent when young, upper surface green, somewhat pale, glabrous, lower surface paler green and sparsely pubescent when mature; midrib flat above and elevated beneath, nerves 8–11 pairs, veinlets reticulate. *Inflorescences* unisexual and staminate or bisexual, thyrsoid, terminal or axillary, staminate flowers clustered in glomerules, main rachis 3.5–4.5 cm long, 0.5–0.6 mm diam, almost glabrous; bisexual ones axillary, racemose, very slender, 6–11 cm long, 0.2–0.6 mm diam, slightly pubescent, often a pistillate flower at top, a



Map 17 Distribution of *Trigonostemon filiformis* Quisumb. (●), *T. merrillii* Elmer (▲), *T. palustris* R.Y.Yu & Welzen (■) and *T. victoriae* R.Y.Yu & Welzen (★).

staminate flower per node below; involucral bracts as stipules; bracts single per node, oblong, 3–9.5 by 0.6–2.2 mm, apex acuminate, green, both sides pubescent. *Staminate flowers* (bud) c. 4 mm diam; pedicel c. 3 mm long, c. 0.3 mm diam, light green, glabrous; sepals elliptic, 1.8–2.5 by 0.6–1.5 mm, white, base connate, margin entire, apex rounded, slightly pubescent outside; petals elliptic, 1.8–2.2 by 1–1.5 mm, dark purple, base cuneate, margin entire, apex acute, both sides glabrous; disc lobes triangular, 0.25–0.35 by 0.25–0.45 mm, apex truncate, c. 0.1 mm thick; stamens 3, androphore c. 0.3 mm long, anthers c. 0.8 mm long, apically divaricate. *Pistillate flowers* c. 4 mm diam; pedicels slightly thickened towards apex, 6.5–7.8 mm long, apically 0.6–0.9 mm diam (apex), pubescent; sepals oblong to lanceolate, 3.3–4 by 1.4–1.7 mm, margin entire, ciliate, apex acute to rounded, pubescent outside, glabrous inside; petals obovate, 4–5 by 2.1–2.9 mm, dark purplish, with a honey mark in the centre, base cuneately narrowed, margin entire, apex rounded, glabrous; disc lobes unequal, rectangular, 0.5 by 0.4–0.9 mm, white, apex truncate, corner rounded, glabrous; ovary c. 0.9 mm diam, densely pubescent; styles 0.1–0.2 mm long; stigma linear, 1.3–1.4 mm long, deeply bifid into 2 arms, each arm 0.9–1.1 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 — Borneo (Sabah)? and Philippines (Luzon).

Note — 1. The description of the fruits is partly based on Quisumbing (1930). *Trigonostemon filiformis* was only known and described from the type collection from Mt. Moises in the last revision (Yu & van Welzen 2018). We found specimens with young staminate flowers and mature pistillate flowers in the forest behind Casapsapan beach in Aurora Province (c. 95 km south of Mt. Moises). The description (both vegetative and reproductive characters) has now been fully updated.

2. *Trigonostemon stenophyllus* was also a poorly known species from Mt. Moises. The species was treated as a doubtful species because no staminate flower was seen in the last revision (Yu & van Welzen 2018). It was considered different from *T. filiformis* by the broader leaves and thicker inflorescences. However, we found a continuous variation between the two species: the leaves can gradually vary from linear (as in the type of *T. filiformis*) to oblong or lanceolate (as in the type of *T. stenophyllus*), and the inflorescences can be very slender and pendulous (as in the type of *T. filiformis*) or thicker and erect (as in the type of *T. stenophyllus*). Therefore, *T. stenophyllus is* synonymised with *T. filiformis*. For illustrations of the typical *T. stenophyllus* and *T. filiformis* see Quisumbing (1930).

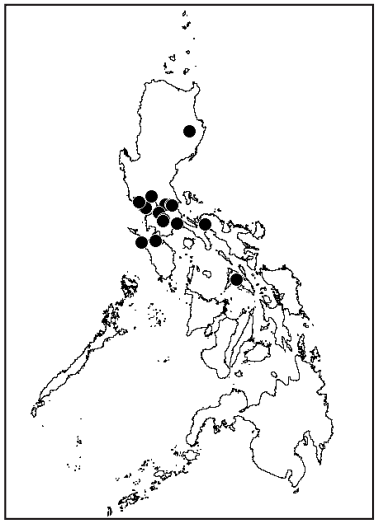
3. The species highly resembles *T. villosus* Hook.f. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen, particularly in the glomerate staminate flowers, but the non-accrescent sepals in the pistillate flower appear to be a useful character to distinguish this species from the latter.

2. ***Trigonostemon longipes*** (Merr.) Merr. — sect. ***Trigonostemon*** — Figure 24; Map 18

Trigonostemon longipes (Merr.) Merr., Philipp. J. Sci. 11, Bot. (1916b) 191; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xiv (1919) 41; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; R.Y.Yu & Welzen, Blumea 62 (2018) 199. — *Dimorphocalyx longipes* Merr., Philipp. J. Sci. 1, Suppl. (1906) 82. — Lectotype (designated by Yu & van Welzen 2018): *FB* (*Whitford*) *1066* (lecto K; isolecto P), Philippines, Luzon, Bataan Prov., Mt. Mariveles.

Trees, up to 6 m tall, stem up to 12 cm diam; flowering branches terete, 1.5–6 mm diam, glabrous or pubescent. *Outer bark* 0.1–0.2 mm thick, reddish or pale brownish, smooth, wrinkled; inner bark 0.1–0.3 mm thick, reddish brown; wood pale yellowish to brown. *Stipules* subulate, 0.5–1 mm long, pubescent at base. *Leaves*: petiole terete but grooved above, 1–11.5

Figure 23 *Trigonostemon stenophyllus* Quisumb., from Casapsapan beach, Casiguran, Aurora, the Philippines. a. Young tree with staminate flowers; b. tree with pistillate flowers; c. bark and wood, showing reddish sap (low



Map 18 Distribution of *Trigonostemon longipes* (Merr.) Merr.

cm long, often slightly thickening towards apex, 0.6–1.8 mm diam (apex), often pubescent when young, glabrous when mature; blade oblong, sometimes oblanceolate, 7.5–18 by 2.5–6 cm, coriaceous, base cuneate, with 1 or 2 pairs of adaxial glands, the inner pair often smaller and caducous or worn away in old leaves, 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 7–11 pairs, curved and connected along margin, veinlets reticulate, often obscure. *Inflorescences* unisexual or bisexual, axillary or terminal, sometimes cauliflorous, thyrsoid, 3–15 cm long, 0.5–1 mm diam, glabrous or slightly pubescent, flowers often only growing in the upper half, some flowers single and cauliflorous; staminate flowers often 4–10 clustered in a glomerule at each node, pistillate flowers often single per node, sometimes only 1 (but up to 5 in extreme cases), pistillate flower present at the apex of the rachis; involucral bracts 2, as stipules; bracts single per node, lanceolate to oblong, 1–3.4 by 0.3–1.1 mm, often pubescent; flowers with a bract and up to 2 bracteoles, triangular, up to c. 1 by 0.6 mm, densely pubescent. *Staminate flowers* 4–4.8 mm diam; pedicel 1.5–2 mm long, 0.4–0.6 mm diam, slightly pubescent; sepals orbicular to elliptic, light green, 1.6–2.5 by 1.3–2 mm, imbricate, base connate, apex rounded, pubescent outside; petals elliptic or spathulate, 2–2.7 by 1.8–3.5 mm, dark red to purple, contorted, base cuneate, margin sometimes ciliate, apex revolute; disc lobes obovate or semi-orbicular, 0.3–0.5 by 0.3–0.5 mm, 0.1–0.15 mm thick, pink, glabrous, apex acute; stamens 5, androphore 0.8–0.9 mm long, 0.1–0.2 mm diam, filament free part c. 0.1 mm long, anthers 0.5–0.6 mm long, yellow, apically divaricate. *Pistillate flowers* c. 6 mm diam; pedicel 2.5–3.5 mm long, thickened towards apex, 0.9–1.2 mm thick (top); sepals orbicular to oblong, light greenish to pinkish, slightly accrescent in fruit, 3.5–4.5 by 2–3 mm, pubescent outside, margin ciliate, apex rounded, sometimes with an apical gland; petals caducous, oblong to spathulate, 2–3.5 by 1.8–3 mm, dark purplish, contorted, glabrous, margin entire, slightly ciliate, apex revolute; disc annular, c. 0.1 mm thick, blackish, glabrous, margin undulate; ovary green, c. 1.2 mm diam, glabrous, stigmas green, deeply bifid, arm

quantity); d. part of a leaf, showing the adaxial glands; e. staminate inflorescence; f. bisexual inflorescence with a pistillate flower at top; g. staminate flower buds; h. pistillate flower, top view; i. pistillate flower, lateral view. — photos by Ren-Yong Yu.

Figure 24 *Trigonostemon longipes* (Merr.) Merr., from Mt. Daraitan, Tanay, Rizal, the Philippines. a. Flowering branch; b. inflorescence; c. infructescence, showing that the plant cohabits with ants; d. staminate flowers, top

0.25–0.3 mm long when flowering, up to 0.1 mm long when fruiting. *Fruits* 0.7–1 cm diam, glabrous; wall 0.4–0.5 mm thick; columella 3.6–4.7 mm long. *Seeds* 4–4.5 mm diam, marbled, hilum rhombic, 0.7–1 by 0.4–0.5 mm.

Distribution — Philippines (endemic).

Habitat & Ecology — Secondary forests, on clay loam or limestone. Altitude: 200–460 m. Flowering: January to April, September; fruiting: January and April.

Notes — Measurements have been updated from the last revision (Yu & van Welzen 2018). Two characters are noteworthy: there are often 2 pairs of adaxial glands at the leaf base and the ovary is certainly glabrous. The species differs from *T. victoriae* in the 3 (vs. 5) stamens and the non-accrescent pistillate sepals (vs. much enlarged in *T. victoriae*). This species is found to cohabit with ants (Figure 24c; RYY and JRC, pers. obs.).

3. ***Trigonostemon merrillii*** Elmer — sect. ***Spinipollen*** — Figure 25; Map 17

Trigonostemon merrillii Elmer, Leafl. Philipp. Bot. 4 (1911) 1304; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 407; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; R.Y.Yu & Welzen, Blumea 62 (2018) 203. — Lectotype (designated here): *Elmer 12819* (lecto L; isolecto BISH*, BM, BO, F*, G*, HBG*, MO*, NY*, US*), Philippines, Palawan, Puerto Princesa, Mt. Pulgar.

Small trees, 1.5–3 m tall, stem up to 2.5 cm diam, hardly branching. *Indumentum* densely sericeous, especially on young parts. *Outer bark* 0.1–0.2 mm thick, pale brownish, sericeous; inner bark 0.3–0.4 mm thick, white to pale yellow, sometimes black when sap is solidified, sap translucent when fresh; wood white to pale yellow; pith sometimes empty. *Stipules* lanceolate to linear, 1–3 mm long, base sericeous, caducous. *Leaves*: petiole terete, often wrinkled when dry, 1–5.5 cm long, 2–6.7 mm diam, densely sericeous; blade elliptic, lower half often cuneately narrowing, 10–46.5 by 7–11.9 cm, chartaceous, base rounded, 2 adaxial glands present but often caducous or 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 with long silky hairs; midrib slightly raised above and much elevated beneath, more densely sericeous, nerves 10–13(–17) pairs, curved and connected near margin, veins and veinlets reticulate, sometimes obscure. *Inflorescences* bisexual or unisexual, paniculate thyrses, up to 31 cm long, 0.4–1.6 mm diam, sericeous; involucral bracts as stipules, nodal bracts lanceolate, variable in size, petiole up to 0.7 cm long, blade 0.4–3.6 by 0.1–0.7 cm, sericeous; staminate flowers partly single and ramiflorous, others glomerate, pistillate flowers single, above or below the staminate ones. *Staminate flowers* 2.8–4.5 mm diam; pedicel 1.5–4.6 mm long, 0.1–0.2 mm diam, pink, glabrescent; sepals unequal, orbicular to elliptic to spathulate, 0.9–1.4 by 0.5–1.2 mm, pink to red in the centre, base connate, margin entire or slightly undulate, apex acute to rounded, more or less pubescent outside; petals spathulate to flabellate, 2–2.9 by 1.5–2.4 mm, dark purple to black, without honey mark, base claw-like, apex rounded to truncate to sometimes slightly bilobed, glabrous on both sides; disc annular, c. 0.25 mm diam (inner margin), c. 0.1 mm thick, red; stamens 3, androphore erect, 0.4–0.5 mm high, anthers ellipsoid, 0.4–0.6 mm long, white, gathered on the top of androphore, slightly divaricate at apex, connective apically with some droplets (expanded cells) with secretion. *Pistillate flowers* (bud) c. 2 mm diam; pedicels 3.5–4.5 mm long, 0.35–4 mm diam (apex), sericeous; sepals elliptic, 1.8–2.2 by 0.7–1.5 mm, entire, apex acute, sericeous outside; petals spathulate, 1.6–2.1 by 1.1–1.2 mm, base cuneate, somewhat claw-like, apex rounded, both

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view; e. staminate flowers, lateral view; f. pistillate flower; g. pistillate flower, petals and a sepal removed, showing the blackish annular disc; h, i. fruit. — a–c, f, g: photos by Ren-Yong Yu; d, e, h, i: photos by John Rey Callado.

Figure 25 *Trigonostemon merrillii* Elmer, from Mt. Saint Paul, Puerto Princesa, Palawan, the Philippines. a. Growing habit; b. main branch with cauliflorous flowers; c. part of paniculate inflorescence with only staminate

sides glabrous; disc lobes annular, less than 0.1 mm thick; ovary c. 0.6 mm diam, smooth or slightly warty, style indiscernible, stigmas partly bifid, arms c. 0.1 mm long, each pair horseshoe shaped. *Fruits* c. 1.25 cm diam, slightly warty; pedicel 1.15–1.35 cm long, 1.2–1.3 mm diam (apex), sepals persistent, not much accrescent, red; columella c. 4 mm long. *Seeds* streaked or conspicuously mottled.

Distribution — Philippines (endemic).

Habitat & Ecology — Lowland dipterocarp forests. Altitude: 15–80 m. Flowering: March.

Note — The first author's (RYY) field observations have provided some new insights for the species: the stem often lacks side-branches and the leaves are clustered at the top of the main branch; the inflorescences can develop into a panicle when mature. The spathulate petals with a claw-like base strongly resemble those of the other species in sect. *Spinipollen*, e.g., *T*. *longifolius* Baill., *T*. *oblongifolius* Merr. The species is known from Palawan and Mindanao. The diameter of fruits is based on Elmer (1911).

4. ***Trigonostemon palustris*** R.Y.Yu & Welzen, *sp*. *nov*. — sect. ***Trigonostemon*** — Figures 26, 27; Map 17

The species resembles the other endemic species in Palawan, *T*. *victoriae*, in the sepals being significantly larger than the petals in pistillate flowers, but it can be distinguished from the latter by the yellow, flat (vs. dark red and revolute) petals and annular disc in both staminate and pistillate flowers (vs. 5 lobes in *T*. *victoriae*). — Type: *Yu 260* (holo PNH; iso L, DLSUH), Philippines, Palawan Province, El Nido, trail to the Nakalit-kalit Waterfalls.

Small trees, c. 2 m tall; flowering branches terete, 3–3.7 mm diam, pubescent in young parts. *Outer bark* grey, 0.1–0.2 mm thick; inner bark 0.1–0.2 mm thick, red, sap red; wood pale yellow. *Stipules* subulate or falcate, 0.7–1.4 mm long, caducous, base pubescent. *Leaves*: petiole terete, slightly thickening towards both ends, 3–7 cm long, 1.6–2 (middle part)–3mm (apex or base) diam, glabrescent; blade elliptic, 12–23 by 5.5–7.7 cm, chartaceous to coriaceous, base acute, 1–2 pairs of adaxial glands present, margin distantly serrate, teeth subulate, apex acuminate to caudate, upper side (somewhat dark) green, glabrous, lower side pale green, often slightly pubescent, particularly on venation; midrib flat or very slightly grooved above, elevated beneath, nerves 8–11 pairs, curved and connected near margin, veins and veinlets reticulate. *Inflorescences* bisexual or unisexual, terminal or axillary, racemose thyrses; main rachis 2–4.5 cm long, 0.6–1.2 mm diam, densely pubescent, few (up to 10) staminate flowers clustered per node, pistillate flowers single per node; involucral bracts as stipules; bracts triangular, 0.7–2.6 by 0.5–0.7 mm, pubescent on both sides. *Staminate flowers* 5–7 mm diam; pedicel 1.5–2 mm long, 0.3–0.4 mm diam, green, slightly pubescent; sepals orbicular to elliptic, 0.8–1.3 by 0.4–0.9 mm, light green, base connate, margin entire, apex rounded to acute, pubescent outside, glabrous inside; petals flabellate, 1.5–1.9 by 1.4–1.6 mm, yellow, base cuneate, margin entire, apex slightly bilobed, glabrous on both sides; disc annular, c. 0.2 mm diam (inner margin), c. 0.2 mm thick, yellow; stamens 3, androphore erect, 0.4–0.5 mm high, anthers ellipsoid, 0.3–0.4 mm long, divaricate at apex. *Pistillate flowers* 4–6 mm diam; pedicel 3.5–5 mm long, thickening towards the apex, 0.6–0.9 mm diam (apex), light greenish to pinkish, pubescent; sepals elliptic, 5–7 by 2–3.5 mm, pink, base connate, margin serrate, apex acuminate, with 3 main teeth; petals obovate to spathulate, 3.4–4.2 by 2.5–3.4 mm, yellow,

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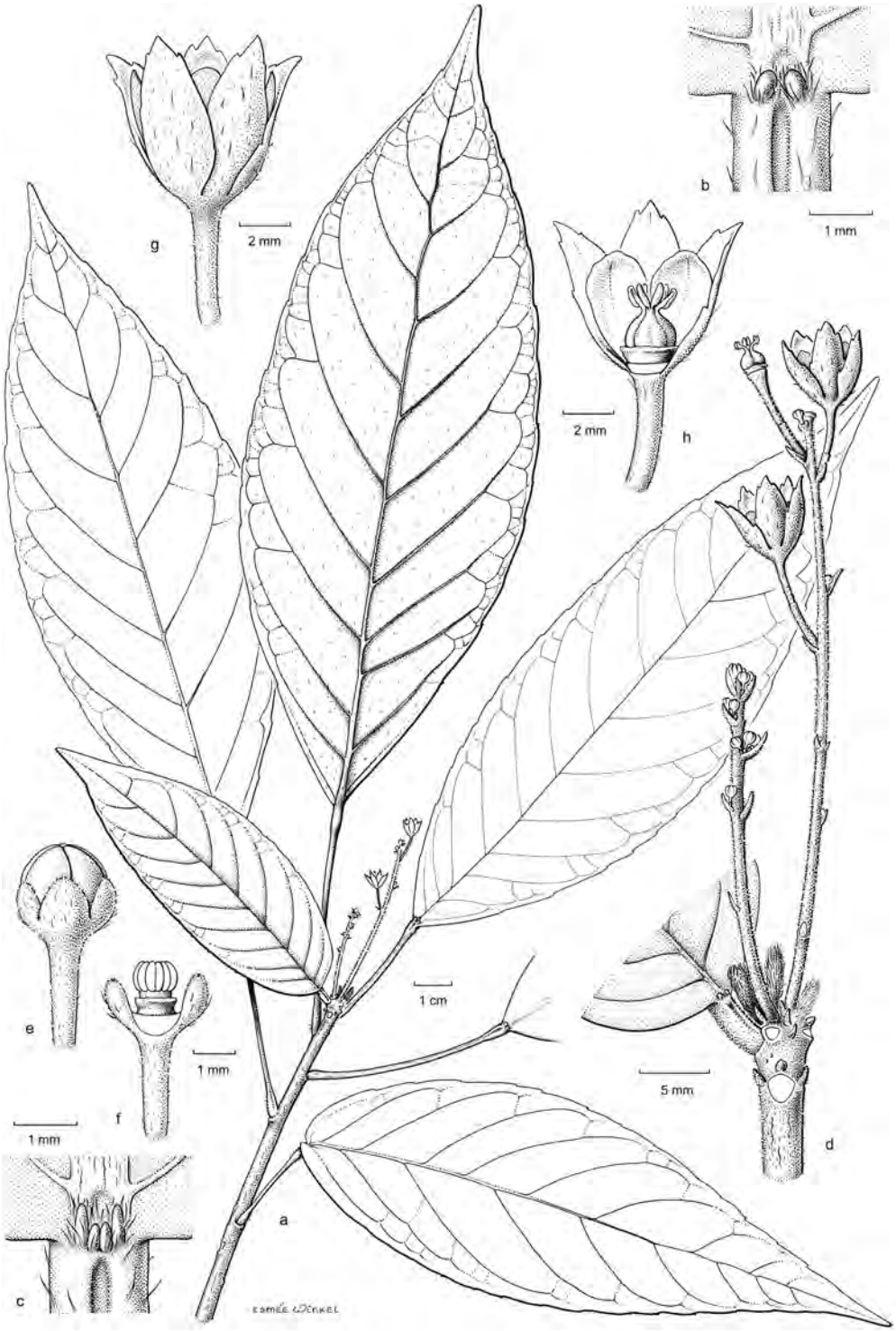
flowers; d. pistillate inflorescence; e. bisexual inflorescence, a pistillate flower at top; f. bisexual inflorescence, pistillate flower at bottom; g. translucent sap; h. staminate flower, lateral view; i. staminate flower, top view; j. juvenile pistillate flower; k. fruit, back side; l. fruit, front side — a, k, l: photos by Danilo Tandang; b–j: photos by Ren-Yong Yu.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base cuneate, apex rounded, sometimes slightly plicate, glabrous on both sides; disc annular, 2.2–2.6 diam, c. 0.1 mm thick; ovary 1.9–2 mm diam, glabrous, style 0.1–0.2 mm long, stigmas completely bifid, arms 0.7–1 mm long. *Fruits* light green, glabrous; sepals persistent, not much accrescent, green, stigmas persistent, pinkish.

Distribution — Philippines (Palawan, endemic).

Habitat & Ecology — Lowland forest edge, in swamps (hence the specific epithet). Altitude: c. 25 m. Flowering: February, April; fruiting: February.

Note — This new species was first brought to our attention by images published on Co's Digital Flora of the Philippines (Pelser et al. 2011 onwards), and we are grateful that the owner of the photos gave us permission to reuse them in this article. The species has two relatively unusual characters: pistillate sepals being larger than petals and yellow petals in both staminate and pistillate flowers. It is the only species with yellow petals in sect. *Trigonostemon*. These characters are only known to occur separately in a few species, e.g., *T. victoriae* (larger sepals than petals in pistillate flowers), and *T. laevigatus* and *T. philippinensis* (yellow petals), but they are all clearly different from this new species. The species is found to cohabit with ants (Figure 27i; RYY pers. obs.).

5. ***Trigonostemon victoriae*** R.Y.Yu & Welzen — sect. ***Trigonostemon*** — Figure 28; Map 17

Trigonostemon victoriae R.Y.Yu & Welzen, Blumea 62 (2018) 215, f. 15. — Type: *PNH* (*Sulit*) *12317* (holo L; iso PNH), Philippines, Palawan Province, Panacan, Aborlan, Victoria Mountains.

Small trees, up to 6 m tall, dbh c. 10 cm; flowering branches (1.5–)2–3 mm diam, pubescent near apical buds and glabrescent in mature parts. *Outer bark* 0.1–0.2 mm thick, brown when young, pale greyish in old parts, somewhat shiny; inner bark 0.1–0.2 mm thick, dark red, sap red; wood pale yellowish. *Stipules* subulate, 0.5–1 mm long, caducous, base pubescent, apex often glabrous. *Leaves*: petiole terete but grooved above, 1–13.5 cm long, 0.8–1.4 mm diam, pubescent when young; blade elliptic to oblong, 8.5–20.5 by 2.5–5.5 cm, chartaceous to coriaceous, base acute, 2 pairs of adaxial glands present, often pubescent, inner pair often smaller, margin distantly serrate, teeth glandular, apex acuminate to slightly caudate, upper side glabrous, green, lower side sparsely pubescent, pale green; venation penninerved, often pubescent on the lower side, midrib more or less raised above and elevated beneath, nerves 5–8 pairs, curved and narrowed along margin, veinlets reticulate. *Inflorescences* unisexual, often terminal or subterminal, involucral bracts as stipules; staminate flowers partly single and cauliflorous, others in racemes, rachis 1–5 cm long, 0.5–0.6 mm diam, appressed pubescent, flowers often only in upper half, bracts lanceolate to triangular, 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 abortive buds below; peduncles 1–5 cm long, 0.5–1 mm diam, pubescent; bracts lanceolate to elliptic, 1–4 by 0.3–0.7 mm, pubescent. *Staminate flowers* 3.7–4.6 mm diam; pedicel 0.5–1.5 mm long, 0.35–0.5 mm diam, pubescent; sepals triangular when young, ovate to elliptic when mature, 1–1.5 by 0.8–1.4 mm, green, imbricate, margin entire, apex acute to acuminate, pubescent outside; petals elliptic, 2.8–3 by 2.3–2.5 mm, dark red, base cuneate, margin entire, apex rounded, glabrous on both sides; disc lobes rhomboid, 0.2–0.25 by 0.3–0.4 mm, c. 0.1 mm thick, fleshy, apex acute; stamens 3, androphore c. 0.7 mm long,

Figure 26 *Trigonostemon palustris* R.Y.Yu & Welzen. a. Flowering branch; b. leaf base, showing 1 pair of adaxial glands; c. leaf base, showing 2 pairs of adaxial glands; d. inflorescences; e. staminate flower bud; f. staminate flower (3 sepals and 5 petals removed); g. pistillate flower; h. pistillate flower (2 sepals and 3 petals removed) (all: *Yu 260*, L). — Drawing by Esmée Winkel, 2019.

Figure 27 *Trigonostemon palustris* R.Y.Yu & Welzen, from Nagkalit-kalit Waterfalls, El Nido, Palawan, the Philippines. a. Growing habit; b. outer bark; c. inner bark and wood, showing reddish sap (low quantity); d. leaf,

anthers ellipsoid, 0.6–0.7 mm long. *Pistillate flowers* 3–4.5 mm diam; pedicel 1.5–3 mm long, 0.4–0.7 mm diam, green, slightly sericeous; sepals lanceolate, 1.6–4 by 0.6–1.6 mm when flowering, accrescent to 10–13 by 2.5–4.5 mm when fruiting, green, 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* c. 1.1 cm diam, sericeous, green; pedicel 1.05–1.25 cm long, thickening towards apex, 1.7–2.2 mm diam (apex), pubescent; sepals persistent, oblong, 9.5–11.2 by 3–4 mm, pubescent on both sides; columella c. 4.6 mm long. *Seeds* not seen.

Distribution — Philippines (Victoria Mountains, endemic).

Habitat & Ecology — Dipterocarp forests, growing on clay, near rivers. Altitude: 78–195 m. Flowering: March to May; fruiting: March to April.

Note — The species is found at the foot of the Victoria Mountains. The petiole can be as long as 13.5 cm, which is similar to *T. longipes*. New descriptions of inflorescences, mature staminate and pistillate flowers and fruits are presented. One of the striking characters of the species is the enlarged sepals in the pistillate flowers. The species is seen to cohabit with ants (Figure 28d, f–h; RYY pers. obs.).

6. ***Trigonostemon villosus*** Hook.f. var. ***merrillianus*** (Airy Shaw) R.Y.Yu & Welzen — sect. ***Trigonostemon*** — Figure 29; Map 19

Trigonostemon villosus Hook.f. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen, Blumea 62 (2018) 218. — *Trigonostemon merrillianus* Airy Shaw, Kew Bull. 25 (1971) 549, non *T. borneensis* Merr., Univ. Calif. Publ. Bot. 15 (1929) 162; Kew Bull., Addit. Ser. 4 (1975) 203. — *Dimorphocalyx* (?) *borneensis* Merr., Philipp. J. Sci. 11, C. Bot. (1916a) 73. — Type: *Hose 420* (holo K; iso L), Sarawak, 4th Division, Baram District, Entoyut River.

Trigonostemon acuminatus Merr., Philipp. J. Sci. 11, Bot. (1916b) 190; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xiv (1919) 41; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 451; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 46. — Type: *BS* (*Ramos*) *24528* (BM, BO, K, L), Philippines, Samar, Catubig River.

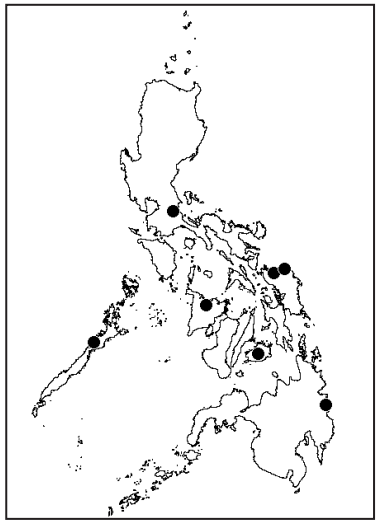
Trigonostemon laxiflorus Merr., Philipp. J. Sci. 16 (1920) 567; Enum. Philipp. Fl. Pl. 2 (1923) 451; Airy Shaw, Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47. — Type: *BS* (*Ramos & Edaño*) *31097* (A*, K, P, US) Philippines.

Small trees, 1–4 m tall, dbh up to 6 cm; flowering branches 2.5–4.5 mm diam, often pubescent when young, glabrescent when mature, buds pubescent. *Outer bark* 0.1–0.2 mm thick, dark brown, sometimes fissured; inner bark 0.1–0.2 mm thick, dark greenish or reddish, sap watery, translucent; wood white. *Stipules* subulate, 0.5–1.9 mm long, base pubescent. *Leaves*: petiole terete but often furrowed above, 1–11 cm long, glabrous to hirsute, sometimes slightly thickened at base and apex, 1.2–2.1 (middle)–3.5 mm (base and apex) diam; blade oblong, 8–29 by 2.2–9 cm, chartaceous, base acute to rounded, 2 adaxial glands present, margin distantly serrate, teeth subulate or glandular, apex acuminate to caudate, upper side glabrous, dark green, lower side paler green, slightly pubescent, particularly on venation; midrib flat or

←

upper side; e. leaf, lower side; f. branchlet and petioles; g. flowering branch; h. staminate inflorescence; i. bisexual inflorescence, showing the plant cohabits with ants; j. staminate flower, top view; k. staminate flower, lateral view; l. pistillate flower; m. pistillate flower, sepals and petals removed, showing the pistil; n. fruit, lateral view, showing accrescent sepals; o. fruit, top view. — a–c, h–m: photos by Ren-Yong Yu; d–g, n, o: photos by P.B. Pelser & J.F. Barcelona (Pelser et al. 2011 onwards).

Figure 28 *Trigonostemon victoriae* R.Y.Yu & Welzen, from Karaniogan River, Narra, Palawan, the Philippines. a. Branch, showing the plant grows on a river bank; b. outer bark; c. inner bark and wood, showing reddish sap; d. branchlet, showing the plant cohabits with ants; e. staminate inflorescence and cauliflorous staminate flower;



Map 19 Distribution of *Trigonostemon villosus* Hook.f. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen

slightly raised above and distinctly elevated beneath, nerves 8–13 pairs, often bow-shaped, connected along margin, veins reticulate, sometimes obscure. *Inflorescences* unisexual, often axillary, staminate flowers partly single and cauliflorous, others clustered in cymes or glomerules, rachis 10–18 cm long, 0.8–1 mm diam, bracts linear to lanceolate, 0.5–10.5 (Palawan) –18 (Samar) by 0.3–3.3 (Palawan) –6.5 (Samar) mm, margin entire, pubescent; pistillate ones racemose, often only 1–3 flowers present at top, rachis 5.5–22 cm long, 0.4 (Mindanao)–0.6–1.3 (Samar and Palawan) mm diam, pubescent, bracts lanceolate, 4.2–11 (Mindanao and Palawan)–19 (Samar) by 0.4 (Mindanao)–2.5–7.3 (Samar and Palawan) mm, margin distantly serrate, teeth glandular, pubescent outside. *Staminate flowers* 5–6.7 mm diam, pedicel 1.3–3 (Palawan)–4.5 (Samar) mm long, 0.2–0.5 mm diam, light green, glabrous; sepals elliptic, 1.2–2 by 0.6–1 mm, imbricate, white, margin ciliate, apex rounded, slightly pubescent outside; petals elliptic, 2.4–3.8 by 1.2–2 mm, purplish black, with a flame-like honey mark in the centre (Palawan), margin entire, apex rounded, glabrous on both sides; disc lobes rectangular or obtrapezoid, 0.25 (Samar)–0.4–0.5 (Palawan) by 0.2 (Samar)–0.45–0.6 (Palawan) mm, yellowish, apex truncate or rounded; stamens 3, androphore 0.5–0.9 mm long, anthers ellipsoid, 0.65 (Samar)–0.9–1.1 (Palawan) mm long, pinkish red, connective apically with numerous reddish droplets with secretion. *Pistillate flowers* 6–8 mm diam, pedicel often slightly thickened towards apex, 5–6 (Palawan)–10.5 (Samar) mm long, apically 0.5–1.5 mm diam, green, appressed pubescent; sepals lanceolate to elliptic, 2–2.4 (Samar)–6.5 (Palawan) by 0.8–2 mm when flowering, sometimes accrescent when fruiting (Palawan), green or red when flowering, red when fruiting, margin serrate, apex acuminate, appressed pubescent outside, sometimes with an apical gland (Palawan); petals as staminate flowers but longer and caducous, 3–3.6 by 1–1.2 mm; disc lobes rectangular, 0.3–0.9 by 0.5–0.6 mm, membranous, apex rounded or truncate; ovary 1–1.1 mm diam, 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; pedicel c. 1.5 cm long, thickening towards apex, c. 1.4 mm diam (apex); sepals persistent, red; wall 0.4–0.5 mm thick; columella 4–6 mm long. *Seeds* globose, c. 5 mm diam, marbled.

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f. staminate flowers, lateral view; g, h. pistillate flowers; i. fruit, lateral view; j. fruit, top view. — photos by Ren-Yong Yu.

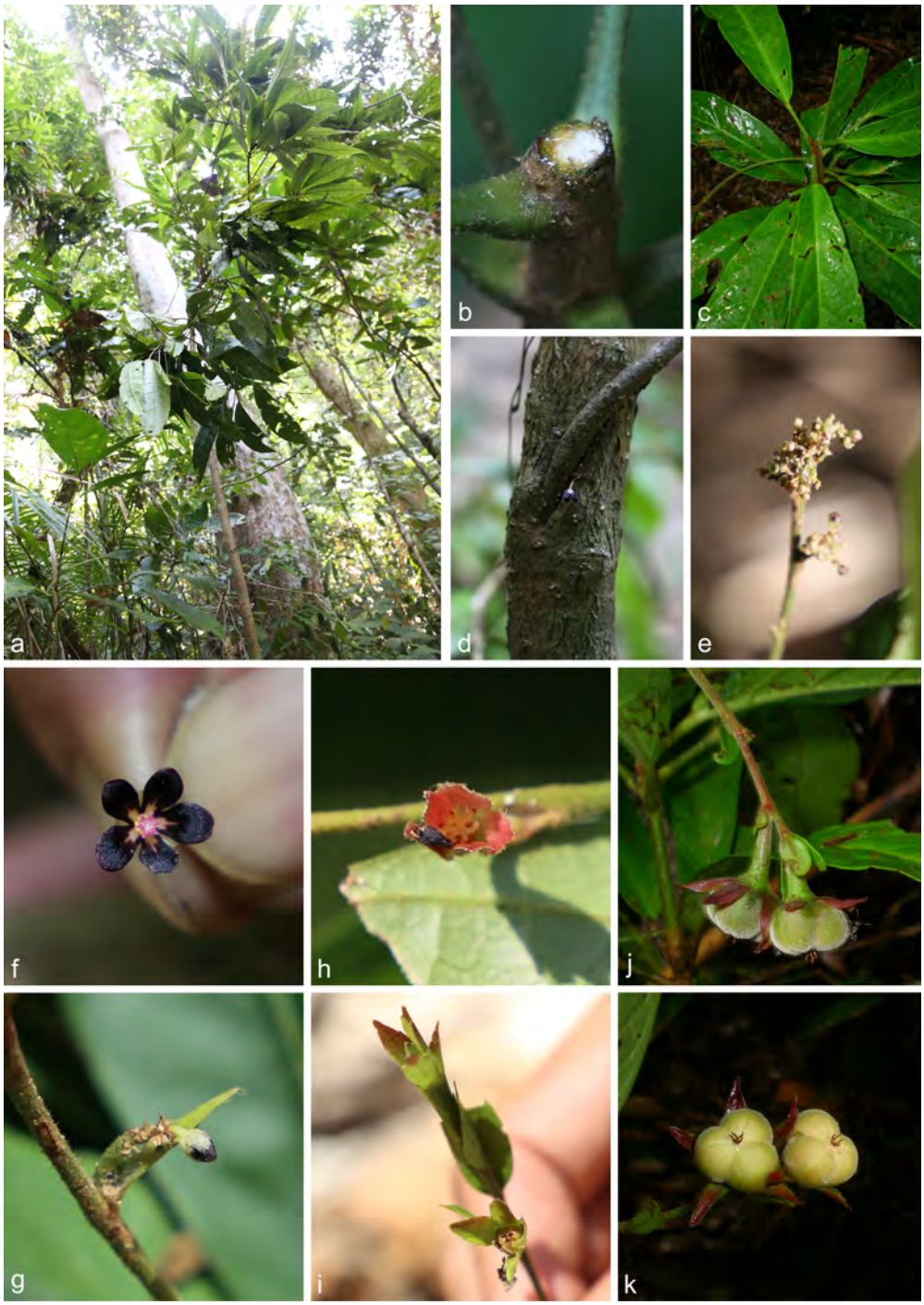

Figure 29 *Trigonostemon villosus* Hook.f. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen, from Mt. Saint Paul, Puerto Princesa, Palawan, the Philippines. a. Growing habit; b. translucent sap; c. branchlet; d. bark with a

Distribution — Borneo and Philippines (new record for Palawan).

Habitat & Ecology — In the Philippines, growing in the understorey of dipterocarp forests, on red clay loam soil, along the coast. Altitude: 10–40 m. Flowering: March to April (Samar and Palawan); May to June (Mindanao). Fruiting: February to March (Samar).

Note — The description is only based on collections from the Philippines. *Trigonostemon villosus* var. *merrillianus* is an extremely variable taxon, but in the Philippines it is less variable in the length of the petiole and the size of the leaf blade. Taxa that are easy to confuse with *T*. *villosus* var. *merrillianus* are *T*. *villosus* var. *borneensis* (differs from the former by the shorter petiole and non-accrescent sepals in the pistillate flowers), *T*. *oblongifolius* (differs by flabellate petals with a claw-like base and lacking a honey mark), *T*. *polyanthus* (differs by the paintbrush-like instead of glomerate staminate inflorescences) and *T*. *filiformis* (differs by the narrower leaf blade, slender inflorescences and non-accrescent sepals in pistillate flowers).

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cauliflorous staminate flower; e. staminate inflorescence; f. staminate flower, top view; g. juvenile staminate flower, lateral view; h. pistillate flower, four of the five petals fallen; i. pistillate flowers, lateral view, petals fallen; j. fruits, lateral view; k. fruits, top view. — a, b, d–i: photos by Ren-Yong Yu; c, j, k: photos by Danilo Tandang.

IDENTIFICATION LIST

Species fully described in text:
1 = *T. filiformis* Quisumb.
2 = *T. longipes* (Merr.) Merr.
3 = *T. merrillii* Elmer
4 = *T. palustris* R.Y.Yu & Welzen
5 = *T. victoriae* R.Y.Yu & Welzen
6 = *T. villosus* Hook.f. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen

Additional Philippine species:
7 = *T. laevigatus* Müll.Arg. var. *laevigatus*
8 = *T. longifolius* Wall. ex Baill.
9 = *T. oblongifolius* Merr.
10 = *T. philippinensis* Stapf
11 = *T. polyanthus* Merr.
12 = *T. villosus* Hook.f. var. *borneensis* (Merr.) Airy Shaw
13 = *T. viridissimus* (Kurz) Airy Shaw var. *viridissimus*
doubtful 14 = *T. angustifolius* Merr.
doubtful 15 = *T. whiteanus* (Croizat) Airy Shaw

Baker 2811: 10; 3295: 10 — BS series 1645: 11; 7257: 7; 10431: 6*; 13965: 9; 15458: 8; 16171: 8; 22018: 7; 22633: 10; 22848: 6; 24528: 6; 24890: 6; 26228: 6; 26911: 2; 28494: 9*; 29167: 6; 30800: 10; 31097: 6; 32424: 6; 33109: 9; 33539: 9; 34041: 2; 36560: 14*; 36612: 7*; 36642: 3*; 36764: 14; 37297: 7; 37326: 7; 39575: 2; 41718: 10; 42630: 6*; 42686: 6; 45242: 8*; 47043: 2; 47205: 10*; 47331: 1; 48717: 2 — Burley 151: 2.
Clemens 16751: 1 — Co 5107: 12.
Elmer 7264: 8; 8326: 10; 12819: 3; 17583: 2; 17600: 10; 18212: 10.
FB series 1066: 2; 1801: 2; 2699: 2; 4153: 3; 13237: 10; 15366: 10; 17733: 15; 19604: 9; 20122: 2 — Fernando 1739: 2.
Iwatsuki P-309: 9.
LBC series 1343: 6; 4305: 2.
Madulid 8394: 7 — Merrill 739: 3; 8198: 8*.
Piper 325: 8* — PNH series 6894: 2; 6895: 10; 6898: 10; 6908: 10; 6910: 2; 9526: 10; 9536: 10; 12317: 5; 14361: 6; 33483: 10; 33511: 10; 34145: 10; 34167: 10; 34196: 10; 34215: 10; 38184: 12; 38399: 3; 39433: 11; 40751: 10; 42096: 8; 42098: 8; 42105: 8; 42283: 8*; 42405: 12*; 42408: 7; 42411: 12; 42416: 12; 91852: 10; 98242: 12; 118089: 10; 169837: 12*; 169838: 12*; 170325: 10 — PPI series 2950: 9*; 12212: 2; 12682: 2; 14746: 9*; 15219: 9*; 17300: 9*; 37553: 6.
Ridsdale 1002: 5.
Santos 4270: 10.
Unknown 3764: 2.
Wenzel 186: 12; 1513: 8; 1616: 10; 1716: 8; 1794: 10; 2706: 6*; 3063: 12; 3322: 12 — R.C. Williams 550: 2 — R.S. Williams 2185: 8.
Yu 226: 2; 227: 2; 230: 2; 240: 1; 242: 1; 243: 1; 247: 5; 248: 5; 249: 5; 251: 6; 252: 6; 253: 6; 254: 6; 255: 3; 256: 3; 257: 3; 258: 5; 260: 4.

Chapter 4 A taxonomic revision of *Trigonostemon* (Euphorbiaceae) outside Malesia

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

Key words

Euphorbiaceae
identification
morphological revision
non-Malesian
taxonomy
Trigonostemon

INTRODUCTION

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

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

For Indochina, a full revision of *Trigonostemon* is still lacking. The first batch of 15 species was presented by Gagnepain in 1922. One year later, he proposed a new genus *Prosartema* Gagnep. (Gagnepain 1924b), mainly based on a difference from *Trigonostemon* in the elongated anthers with a conical appendix. In the following year (Gagnepain 1925a), a new species was described for *Prosartema* and another new genus, *Poilaniella* Gagnep., was proposed. *Poilaniella* differs from *Trigonostemon* mainly in the cupular disc, sessile anthers and short cymes with non-fascicled flowers. These two genera, however, were both synonymised with *Trigonostemon* in later treatments (e.g., Airy Shaw 1978, Yu & van Welzen 2018). Two more species were also described for *Trigonostemon* in the same year (Gagnepain 1925a). All these taxa (three genera and 22 species) were considered as endemic to Indochina at that time. Later in this year, Gagnepain (1925b) transferred *T. laoticus* Gagnep. to *Prosartema*, and newly recorded two *Trigonostemon* species originally only known for Thailand for the Indochinese flora. Therefore, a total of 24 species (18 under *Trigonostemon*, three under *Prosartema* and one under *Poilaniella*) were accepted for Indochina (Gagnepain 1925b), and this forms our basic knowledge of the plants in this area. Recently, four species were added to the flora of Vietnam (Hộ 1992) and one species was newly described (Tagane et al. 2017). Because Hộ (1992) followed Airy Shaw's (1969) generic circumscription of *Trigonostemon* (for details see Yu & van Welzen 2018), two species of *Tritaxis* Baill. (as *Trigonostemon annamensis* (A.Chev.) P.H.Hô (basionym *Tritaxis annamensis* A.Chev. was not published) and *Trigonostemon gaudichaudii* (Baill.) Müll.Arg.) were also included in his work.

Thailand shares a large proportion of species with the adjacent areas. Only four species were newly described for Thailand (Craib 1911, 1924; Airy Shaw 1971). Another nine species were recorded for Thailand by Craib (1911) and Airy Shaw (1969, 1972a). On the basis of Airy Shaw's (1972a) treatment, Chantaranothai (2005) added one more species to the flora of Thailand; therefore, a total of 14 species (two endemic) were accepted for the Flora of Thailand (Chantaranothai 2007). Thailand and Indochina neighbour each other and it is seems odd that the numbers of newly described species in the early years (before 1925) are in striking contrast

(2 vs 24, respectively). This likely reflects a difference in the species concepts of the authors: Craib was seemingly more conservative than Gagnepain.

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

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

Key to the species of India* (*including Andaman & Nicobar Islands*), *Sri Lanka and Bangladesh
(couplet 5 partly according to Balakrishnan & Chakrabarty 1991; couplet 6 partly according to Talukdar et al. 2015)

1. Venation pinnate 2
1. Venation triplinerved 6

2. Flowers partly (at least staminate ones) cauliflorous 3
2. Flowers never cauliflorous, inflorescences axillary or terminal 4

3. Leaf blade elliptic to oblong, lower part narrow-rounded; petals orange .. 2. *T. aurantiacus*
3. Leaf blade oblanceolate, lower part cuneately narrowed; petals purple.....
..... 26. *T. semperflorens*

4. Pistillate sepals without a gland or appendage outside. — Great Nicobar island .....
..... 29. *T. villosus* var. *nicobaricus*
4. Pistillate sepals (check multiple sepals) with a gland or appendage outside. — Travancore and Sri Lanka..... 5

5. Petals bilobed; stigmas twice-bifid. — Sri Lanka .....7. *T. diplopetalus*
5. Petals not bilobed; stigmas bifid. — Travancore and Sri Lanka ..... 21. *T. nemoralis*

6. Inflorescences shorter than 2 cm..... 19. *T. montanus*
6. Inflorescences longer, up to 12 cm long .....30a. *T. viridissimus* var. *viridissimus*

Key to the species of Myanmar

1. Venation pinnate 2
1. Venation triplinerved 7

2. Petioles shorter than 3.5 cm 3
2. Petioles of at least some leaves longer than 3.5 cm 4

3. Flowers mostly cauliflorous, inflorescences cymes or thyrses (with side branches); pistillate sepals accrescent; fruits smooth ..... 9. *T. flavidus*
3. Flowers never cauliflorous, inflorescences axillary or terminal, racemes or racemose thyrses (without side branches); pistillate sepals not accrescent, fruits more or less warty ..... 17. *T. longifolius*

4. Inflorescences paniculate. — Mandalay ..... 23. *T. philippinensis*
4. Inflorescences racemes or racemose thyrses. — Tenasserim and Amherst 5

5. Pistillate sepals not accrescent. — Amherst ..... 18. *T. malaccanus*
5. Pistillate sepals accrescent. — Tenasserim 6

6. Disc of 5 glands or lobes; pistillate sepals fringed with capitate glands . 11. *T. heteranthus*
6. Disc annular; pistillate sepals with a mostly entire margin but with 2 teeth near apex ..... 15. *T. lanceolatus*

7. Staminate flower buds globose; fruits hirsute. — Sagaing and Kachin ..... 24. *T. quocensis*
7. Staminate flower buds conical; fruits glabrous. — Mergui and Tenasserim ..... 30a. *T. viridissimus* var. *viridissimus*

Key to the species of China

1. Leaf blades pubescent above 2
1. Leaf blades glabrous to slightly pubescent above 4

2. Venation pinnate; petals reddish purple to black, flowers mostly cauliflorous . 9. *T. flavidus*
2. Venation triplinerved or palmate; petals yellow to orange; flowers never cauliflorous 3

3. Disc glabrous; fruits 1.05–1.3 cm diam, smooth ..... 1. *T. adenocalyx*
3. Disc pubescent; fruits c. 3 cm diam, warty ..... 27. *T. tuberculatus*

4. Domatia present on the lower surface of at least some leaves ..... 10. *T. fragilis*
4. Domatia absent 5

5. Venation pinnate 6
5. Venation triplinerved 8

6. Petioles of at lease some leaves longer than 3.5 cm ..... 23. *T. philippinensis*
6. Petioles shorter than 3.5 cm 7

7. Petals dark purplish; staminate inflorescences racemose thyrses, never cauliflorous ..... 17. *T. longifolius*
7. Petals orange; staminate inflorescences condensed cymes or thyrses, always cauliflorous ..... 31. *T. xyphophylloides*

8. Inflorescences (when mature) often longer than 13 cm 9
8. Inflorescences up to 13 cm long 10

9. Petals white; style often indistinct, 0.1–0.2 mm long ..... 8. *T. eberhardtii*
9. Petals yellow to orange; style 0.2–0.7 mm long ..... 30. *T. viridissimus*

10. Translucent (oil?) dots often present in green parts; indistinctively triplinerved; inflorescence axis very slender, up to 0.5 mm diam; often only a few flower buds present in the inflorescences in herbarium specimens. — Guangxi ..... 3. *T. bonianus*
10. Translucent (oil?) dots absent in green parts; distinctively triplinerved; inflorescence axis stronger, up to 1 mm diam; often a large number of flowers present in the inflorescences in herbarium specimens. — Yunnan ..... 16. *T. lii*

Key to the species of Thailand

1. Petioles shorter than 3.5 cm 2
1. Petioles of at least some leaves longer than 3.5 cm 12

2. Leaf blades pubescent above 3
2. Leaf blades glabrous to slightly pubescent above 4

3. Indumentum of only simple hairs; flowers mostly cauliflorous ..... 9. *T. flavidus*
3. Indumentum of simple and stellately bundled hairs; flowers never cauliflorous ..... 25. *T. reidioides*

4. Petals yellow, orange or light pink 5
4. Petals white, dark pink, dark red to purplish black 7

5. Staminate flowers cauliflorous; filaments fully connate; anthers divaricate at apex ..... 2. *T. aurantiacus*
5. Flowers never cauliflorous; filaments often with a free part; anthers not divaricate 6

6. Translucent (oil?) dots absent in green parts; leaves glabrous on the lower surface; petals bilobed ..... 14. *T. laevigatus*
6. Translucent (oil?) dots present in green parts; leaves sparsely pubescent on the lower surface; petals with an entire margin ..... 30a. *T. viridissimus* var. *viridissimus*

7. Stamens 5 8
7. Stamens 3 9

8. Inflorescences often longer than 1.5 cm (staminate 4–8 cm, pistillate 1–15 cm) ..... 4. *T. capillipes*
8. Inflorescences shorter, up to 1.5 cm long ..... 22. *T. pachyphyllus*

9. Disc annular 10
9. Disc of 5 glands or lobes 11

10. Indumentum of only simple hairs; inflorescences racemes or racemose thyrses..... ..... 17. *T. longifolius*
10. Indumentum of simple and stellately bundled hairs; inflorescences paniculate thyrses..... ..... 25. *T. reidioides*

11. Pistillate sepals fringed with capitate glands; fruits glabrous..... 13. *T. kerrii*
11. Pistillate sepals with an entire margin; fruits pubescent ..... 20. *T. murtonii*

12. Inflorescences paniculate thyrses (with side branches) 13
12. Inflorescences racemose thyrses (without side branches)..... 15

13. Filaments fully connate; anthers divaricate at apex..... 23. *T. philippinensis*
13. Filaments often with an apical free part; anthers not divaricate..... 14

14. Petals white (or rarely yellow), staminate flower buds often conical; fruits glabrous..... ..... 8. *T. eberhardtii*
14. Petals yellow, staminate flower buds globose; fruits hirsute.....24. *T. quocensis*

15. Stamens 5..... 28. *T. verticillatus*
15. Stamens 3..... 16

16. Pistillate sepals accrescent.....15. *T. lanceolatus*
16. Pistillate sepals not accrescent.....18. *T. malaccanus*

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

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

1. Venation pinnate 2
1. Venation triplinerved 7

2. Petioles shorter than 3.5 cm 2
2. Petioles of at least some leaves longer than 3.5 cm 6

3. Leaves pubescent above; flowers mostly cauliflorous.....9. *T. flavidus*
3. Leaves glabrous to slightly pubescent above; flowers never cauliflorous 4

4. Inflorescence longer, up to 30(–55 in extreme cases) cm long; disc annular .....17. *T. longifolius*
4. Inflorescence up to 11.2 cm long; disc of 5 glands or lobes 5

5. Pistillate sepals fringed with capitate glands; fruits glabrous..... 13. *T. kerrii*
5. Pistillate sepals with an entire margin; fruits pubescent ..... 20. *T. murtonii*

6. Inflorescences racemose thyrses; pistillate sepals accrescent; fruits densely hirsute, smooth .....15. *T. lanceolatus*
6. Inflorescences paniculate; pistillate sepals not accrescent fruits glabrous, warty .... 23. *T. philippinensis*

7. Indumentum of simple and stellately bundled hairs ..... 25. *T. reidioides*
7. Indumentum of only simple hairs 8

8. Domatia present on the lower surface of at least some leaves ..... 10. *T. fragilis*
8. Domatia absent 9

9. Translucent (oil?) dots absent in green parts ..... 16. *T. lii*
9. Translucent (oil?) dots present in green parts 10

10. Petals white ..... 8. *T. eberhardtii*
10. Petals yellow to orange 11

11. Inflorescence axis very slender, up to 0.5 mm diam; often only a few very flower buds present in the inflorescences in herbarium specimens ..... 3. *T. bonianus*
11. Inflorescence axis stronger, up to 2 mm diam, often a large number of flowers present in the inflorescences in herbarium specimens 12

12. Staminate flower buds globose; fruits hirsute ..... 24. *T. quocensis*
12. Staminate flower buds conical; fruits glabrous 13

13. Fruits more or less warty ..... 5. *T. capitellatus*
13. Fruits smooth ..... 30. *T. viridissimus*

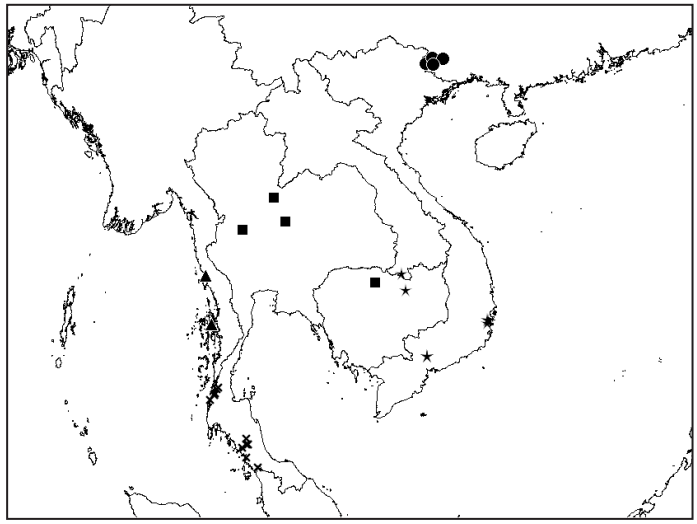
TAXONOMY

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

1. ***Trigonostemon adenocalyx*** Gagnep. — sect. ***Tylosepalum*** — Map 20

Trigonostemon adenocalyx Gagnep., Bull. Soc. Bot. France 69 (1922) 747; in Lecomte, Fl. Indo-Chine 5 (1925b) 319. — Type: *Unknown collector* (P, barcode P00717084), Indochina?
Trigonostemon lutescens Y.T.Chang & J.Y.Liang in Y.T.Chang, Guihaia 3 (1983) 173, f. — Type: *Longgang Exped. 12083* (IBK, barcodes IBK00169526, IBK00190787), China, Guangxi, Longgang Natural Reserve.

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



Map 20 Distribution of *Trigonostemon adenocalyx* Gagnep. (●), *T. capillipes* (Hook.f.) Airy Shaw (×), *T. capitellatus* Gagnep. (★), *T. heteranthus* Wight (▲) and *T. kerrii* Craib (■).

mm, base connate, margin entire, apex acute to rounded, sometimes with a notch and an adaxial gland, slightly pubescent outside; petals flabellate, 4–7.2 by 1.7–4.5 mm, base claw-like, apex rounded, yellow to orange, glabrous; disc annular, 0.2–0.3 mm wide; stamens 3, androphore 0.9–1.7 mm long, 0.15–0.2 mm diam, filament free part 0.3–0.5 mm long, anthers ellipsoid, 0.5–0.6 mm long. *Pistillate flowers* c. 8 mm diam; buds conical; pedicel 1–1.5 cm long, 1–1.1 mm diam, pubescent; sepals lanceolate, 3–7 by 1–1.8 mm, apex acuminate; petals as staminate flowers; disc annular, c. 0.5 mm wide; ovary 0.9–1.2 mm diam, glabrous, style absent, stigmas 0.7–1.2 mm long, apically not bifid but thickened. *Fruits* 1.05–1.3 cm diam, glabrous, smooth, sometimes marbled; pedicel 0.8–1.7 cm long, 1.3–1.7 mm diam (apex); sepals persistent, very slightly or not accrescent; columella 4.5–6 mm long. *Seeds* not seen.

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

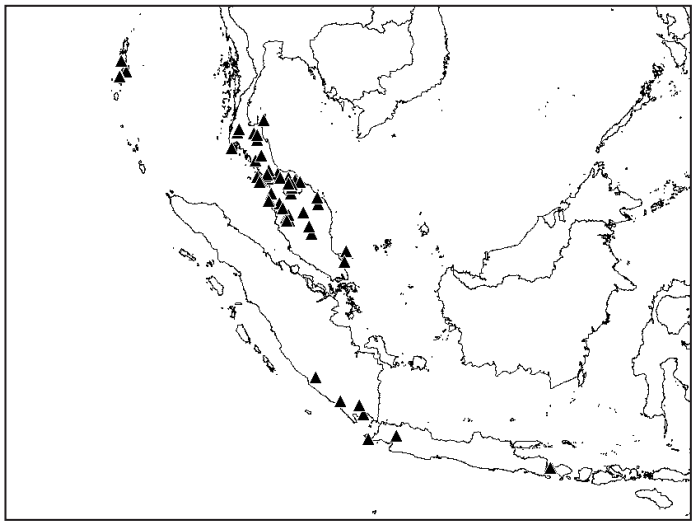
Habitat & Ecology — In forests, growing on limestone. Elevation: 280–400 m. Flowering: April to May; fruiting: April and August.

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

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

2. ***Trigonostemon aurantiacus*** (Kurz ex Teijsm. & Binn.) Boerl. — sect. ***Tylosepalum*** — Map 21

Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 284; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 93; in Engl. & Harms, Pflanzenfam. ed. 2, 19c (1931) 170; Jabl., Brittonia 15 (1963) 164, in obs.; Airy Shaw, Kew Bull. 23 (1969) 126; Kew Bull. 26 (1972a) 345, f. 11; Whitmore, Tree Fl. Malaya 2 (1973) 136; Airy Shaw, Hooker´s Icon. Pl. 38 (1974) t. 3721; Kew Bull. 36 (1981) 352; N.P.Balakr. & Chakrab., Candollea 46 (1991) 610, f. 1; Chantar. in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007)



Map 21 Distribution of *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl.

576; R.Y.Yu & Welzen, Blumea 62 (2018) 187, f. 1. — *Tylosepalum aurantiacum* Kurz ex Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 27 (1864) 50. — *Codiaeum aurantiacum* (Kurz ex Teijsm. & Binn.) Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1118. — Lectotype (designated by Yu & van Welzen 2018): *Teijsmann s.n*. (lecto L, barcode L.2260196), Indonesia, Java, cultivated in Bogor Botanical Garden (originally from Bangka?).

Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl. var. *rubriflorus* N.P.Balakr. & Chakrab., J. Econ. Taxon. Bot. 5 (1984a) 169; Chakrab., J. Econ. Taxon. Bot. 6 (1985) 498. — Type: *Ansari 1361A* (holo CAL, barcode CAL0000023655), *Ansari 1361B* (iso PBL, not seen), *Ansari 1361C* (iso PBL, not seen), *Ansari 1361D* (iso PBL, not seen), *Ansari 1361E* (iso PBL, not seen), *Ansari 1361F* (iso PBL, not seen), India, South Andamans, Havelock Islands.

Description and taxonomic notes see Yu & van Welzen 2018.
Distribution — India (South Andamans), Thailand, Malay Peninsula, Sumatra, Java, Bali.

3. ***Trigonostemon bonianus*** Gagnep. — sect. ***Tylosepalum*** — Map 22

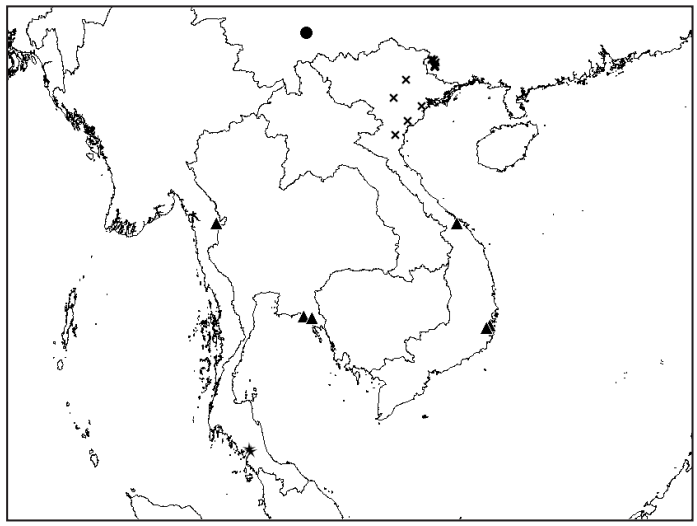
Trigonostemon bonianus Gagnep., Bull. Soc. Bot. France 69 (1922) 747; in Lecomte, Fl. Indo-Chine 5 (1925b) 314. — Lectotype (designated by Li et al. 2006): *Bon 718* (lecto P, barcode P00717086), Vietnam, Mt. Trui.

Trigonostemon petelotii Merr., Univ. Calif. Publ. Bot. 10 (1924) 425. — Type: *Pételot 795* (A, barcode A00048876, P, barcodes P00648663, P00648664, UC*, barcode UC223795), Vietnam, Cho-Ganh.

Trigonostemon filipes Y.T.Chang & X.L.Mo in Y.T.Chang, Acta Phytotax. Sin. 27 (1989) 149; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 169. — Type: *Longgang Exped*. *12240* (holo IBK, barcode IBK00169515; iso MO, barcode MO934096), China, Guangxi, Longgang Natural Reserve.

Trigonostemon kwangsiensis Hand.-Mazz. var. *viridulis* Hand.-Mazz. var. viridulis H.S.Kiu in H.S.Kiu & X.X.Chen, Guihaia 12 (1992) 211. — Type: *Liang 66719* (holo IBSC, barcode IBSC0306903; iso IBK, barcodes IBK00169523, IBK00169525), China, Guangxi, Longzhou, Shangjin, Longhushan.

Shrubs, 0.5–3 m tall; flowering branches 1–2 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts. *Bark* c. 0.1 mm thick, white when young, dark brown to black when mature; wood pale yellow. *Stipules* subulate, 0.3–0.9 mm long, caducous, pubescent at base. *Leaves*: petiole terete but grooved above, sometimes thickened at apex and base, 0.4–4 cm long, middle part 0.6–1.1 mm diam, pubescent; blade elliptic to oblong, 5.5–16 by 1.7–6.1 cm, somewhat thin-chartaceous, base acute to rounded, 1 or 2 pairs of adaxial glands present, often caducous, margin distantly serrate, teeth falcate, apex acuminate to caudate, upper surface glabrous or glabrescent, lower surface sparsely pubescent; venation indistinctively triplinerved, midrib slightly raised above and distinctively elevated and pubescent beneath, secondary veins 5–8 pairs, connected along margin, tertiary veins scalariform, veinlets reticulate, sometimes obscure. *Inflorescences* bisexual, often terminal, paniculate thyrses, often only a few flower buds present in the inflorescences in herbarium specimens; main axis terete, 3–13 cm long, (0.2–)0.4–0.5 mm diam, often slightly pubescent; involucral bracts as stipules; bracts linear to lanceolate to triangular, 0.2–3.5 by 0.2–0.6 mm, pubescent. *Staminate flowers* (bud) c. 2 mm diam; pedicel 0.8–3.9 mm long, 0.15–0.2 mm diam, glabrous to slightly pubescent; sepals elliptic to ovate, 0.7–1.5 by 0.3–1 mm, base connate, margin entire, apex acute, sometimes with a notch and/or an adaxial gland, pubescent outside; petals orbicular, 1.3–1.6 by 1–1.3 mm, yellow, apex rounded, glabrous; disc annular, margin undulate, c. 0.3 mm wide; stamens 3, androphore very short, indistinct, anthers globose to ellipsoid, 0.5–0.6 mm long. *Pistillate flowers* c. 8 mm diam; pedicel slightly thickened toward apex, 4.8–11.3 mm long, apically 0.6–0.9 mm diam when flowering, pubescent; sepals elliptic, 2–2.9 by 1–1.3 mm, apex acute, sometimes with a notch and an adaxial gland; petals as staminate flowers; disc annular, c. 0.4 mm wide, margin undulate; ovary c. 2.2 mm diam, glabrous, style c. 0.3 mm long, stigmas c. 0.5 mm long, not bifid. *Fruits* 0.8–1.1 cm diam, glabrous; pedicel 1.2–2.2 cm long, 1.2–1.5 mm diam (apex); sepals persistent but not accrescent; wall 0.3–0.5 mm thick, exocarp partly detaching; columella 5.7–7.7 mm long. *Seeds* 6.3–6.7 mm diam, marbled; hilum rhombic, 0.9–1.3 by 0.7–0.9 mm.



Map 22 Distribution of *Trigonostemon bonianus* Gagnep. (×), *T. lanceolatus* (S.Moore) Pax (▲), *T. pachyphyllus* Airy Shaw (⋆) and *T. tuberculatus* F.Du & Ju He (●).

Distribution — China (Guangxi) and Vietnam.

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

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

4. ***Trigonostemon capillipes*** (Hook.f.) Airy Shaw — sect. ***Trigonostemon*** — Map 20

Trigonostemon capillipes (Hook.f.) Airy Shaw, Kew Bull. 20 (1967) 413; Kew Bull. 26 (1972a) 345; Whitmore, Tree Fl. Malaya 2 (1973) 135; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 202; R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 29, in key, 45; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 24; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 576; R.Y.Yu & Welzen, Blumea 62 (2018) 191. — *Dimorphocalyx capillipes* Hook.f. (1887) 404; Pax & K.Hoffm. in Engl. (1911) 33; Ridl. (1924) 266. — Type: *Lobb s.n*. (K, barcode K000894763), Singapore.

Description and taxonomic notes see Yu & van Welzen 2018.

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

5. ***Trigonostemon capitellatus*** Gagnep. — sect. ***Tylosepalum*** — Map 20

Trigonostemon capitellatus Gagnep., Bull. Soc. Bot. France 69 (1922) 748; in Lecomte, Fl. Indo-Chine 5 (1925b) 311. — Lectotype (designated here): *Pierre 1323* (lecto P, barcode P00717092; isolecto K barcode K000959315, P barcodes P00717090, P00717091, US00433339), Vietnam, Bien Hoa, towards Dongnai river near Tri Huyen. Other syntypes: *Thorel s.n*. (P, barcode P00717089), Laos, Île de Khon; *Pierre 472* (P barcode P00717093), Vietnam, Bien Hoa, towards Dongnai river near Tri Huyen.

Trigonostemon cochinchinensis Gagnep., Bull. Soc. Bot. France 69 (1922) 748; in Lecomte, Fl. Indo-Chine 5 (1925b) 311, *syn. nov*. — Type: *Pierre 1869* (K, barcode K000959316, P, barcodes P00717094, P00717095, P00717096), Vietnam, Bao Chiang.

Trigonostemon thorelii Gagnep., Bull. Soc. Bot. France 69 (1922) 755; in Lecomte, Fl. Indo-Chine 5 (1925b) 315, *syn. nov*. — Type: *Thorel 2264* (A, barcode A00048877, P, barcodes P00648671, P00648672, P00717148), Laos, Stung Tréng à Kong.

Trigonostemon verrucosus J.J.Sm., Bull. Jard. Bot. Buitenzorg ser. 3, 6 (1924) 97, *syn. nov*. — Type: *Bogor Botanical Garden VIII.E.16* (BO, sheets no. BO1298241, BO1298242, BO1298243, IBSC, barcode IBSC0306957, K, barcode K000959299, L, barcode L.2258669, SING, U, barcode U0002105), Java, cultivated in Bogor Botanical Garden.

Shrubs, 1.5–3 m tall, dbh 2–3 cm; flowering branches 1.3–3.7 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts. *Outer bark* 0.1–0.2 mm thick, very finely roughened, brown, grey or black; inner bark 0.1–0.2 mm thick, dark red; wood pale yellowish, pith sometimes hollow. *Stipules* very small, often indistinct, pointing or subulate, 0.2–0.4 mm long, pubescent at base, caducous. *Leaves*: petiole terete but flat or slightly furrowed above, 0.3–2.3 cm long, 0.6–1.5 mm diam, pubescent; blade elliptic to oblong, 6–17.6 by 2–6.2 cm, chartaceous, base acute to rounded, 2 adaxial glands present, margin entire, apex acuminate to slightly caudate, upper surface glabrous, dark glossy green, lower surface more or less pubescent especially along venation and margin, bright light green; venation distinctly triplinerved, midrib and basal secondary veins slightly raised above, distinctly elevated beneath, other secondary veins 3–6 pairs,

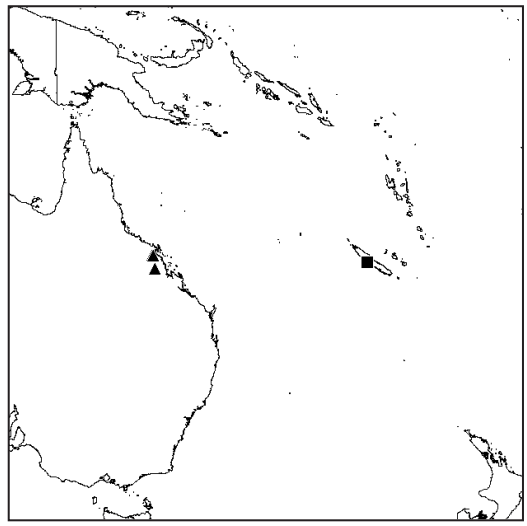
veinlets reticulate, sometimes obscure. *Inflorescences* bisexual, often axillary panicles; main axis up to 21 cm long, 0.5–1 mm diam, green, pubescent; bracts lanceolate, up to 3 by 0.5 mm, pubescent. *Staminate flowers* 3.5–5.5 mm diam; buds conical; pedicels 2.5–4.4 mm long, 0.15–0.3 mm diam, glabrescent; sepals elliptic to somewhat rectangular, 0.6–0.8 by 0.5–0.7 mm, apex truncate or slightly emarginate, glabrescent outside, with an apical gland outside; petals obovate, 2–3.2 by 1.2–1.7 mm, pale light to dull ochre yellow, contort, apex rounded, glabrous; disc annular, 0.2–0.3 mm wide, 0.5–0.7 mm diam, glossy dark yellow, margin undulate, glabrous; stamens 3, androphore erect, 0.7–1.2 mm long, 0.1–0.15 mm diam, white, trifid at apex, free filament part 0.2– 0.3 mm long, white, anthers free, subglobose, 0.35–0.6 mm long, cream. *Pistillate flowers* c. 5 mm diam; buds conical; pedicels as staminate flower but thickened toward apex, 5–7 mm long, apically 0.5–0.6 mm diam when flowering, accrescent up to 1.5 cm long and 1.5 mm diam in fruit; sepals as in staminate flowers but sometimes lanceolate, apex sometimes acute, sometimes with more hairs, especially near gland; petals as staminate flowers but caducous when fruiting; disc as in staminate flowers; ovary 0.7–0.8 mm diam, glabrous and sometimes gibbose, style 0.1–0.2 mm long, stigmas 0.6–1 mm long, apically very slightly bifid and thickened. *Fruits* 0.95–1 cm diam, glabrous, more or less warty; sepals persistent but not accrescent; wall 0.3–0.5 mm thick, exocarp partly detaching; columella 3–5 mm long. *Seeds* 5.2–6.2 mm diam, dark brownish when dry, sometimes marbled, hilum oblong to orbicular, 0.6–1.2 by 0.3–0.9 mm.

Distribution — Cambodia, Laos, Vietnam.

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

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

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



Map 23 Distribution of *Trigonostemon cherrieri* J.M.Veillon (■) and *T. inopinatus* Airy Shaw (▲).

6. ***Trigonostemon cherrieri*** J.M.Veillon — sect. ***Tylosepalum*** — Map 23

Trigonostemon cherrieri J.M.Veillon, Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4 (1992) 55. — Type: *Veillon 7385* (holo P, barcode P00057693; iso: K, barcode K000959366, L, barcode L0016479, P, barcodes P00057694, P00057695, P00057696, MO*, barcode MO260396, NOU*, barcodes NOU005872, NOU005874), New Caledonia, Poya, south of Mepouiri, not far from the coast.

Shrubs, 2–4 m tall; flowering branches 0.8–3.5 mm diam, pubescent when young, glabrous in old parts. *Outer bark* 0.1–0.2 mm thick, pale brown to grey; inner bark 0.1–0.2 mm thick, reddish brown; wood pale yellowish. *Stipules* subulate, 0.15–0.3 mm long, caducous, often indistinct, pubescent at base. *Leaves*: petiole terete, grooved above, 0.5–2.2 cm long, 0.7–1.4 mm diam, sparsely pubescent or glabrous; blade elliptic, 3.5–11.5 by 1.8–4.9 cm, coriaceous, base acute to rounded, 2 adaxial glands present, margin entire, apex rounded, occasionally with a short notch, both surfaces glabrescent; venation pinnate, midrib flat above and elevated beneath, base slightly pubescent beneath when young, secondary veins 4–8 pairs, curved and connected along margin, tertiary veins reticulate, often obscure. *Inflorescences* bisexual or unisexual, terminal or axillary or cauliflorous, fascicled cymes or racemose thyrses; axis terete, up to 5.5 cm long, 0.5–1.1 mm diam, slightly pubescent, 1 or 2 pistillate flowers at apex, staminate flowers below; bracts lanceolate, 0.5–2.4 by 0.15–0.5 mm, pubescent outside. *Staminate flowers* 4.2–5.3 mm diam; pedicel 3.8–7.4 mm long, 0.3–0.5 mm diam, slightly pubescent; sepals elliptic to lanceolate, 1.2–2.1 by 0.3–1.2 mm, base connate, margin entire, apex acute to rounded, pubescent outside; petals obovate, 2–3.2 by 1.3–1.7 mm, yellow, glabrous; disc lobes semi-orbicular, c. 0.2 by 0.4 mm diam, apex rounded; stamens 3, androphore c. 1.6 mm long, c. 0.15 mm diam, anthers ellipsoid, 0.5–0.7 mm long. *Pistillate flowers* (fruiting) c. 2.5 mm diam; pedicel 1.1–1.7 cm long, 0.7–0.8 mm diam, glabrescent; sepals lanceolate to elliptic, 1.5–2.5 by 0.7–1.5 mm, margin entire, apex rounded to acute to sometimes acuminate; petals elliptic, 4–4.3 by 0.7–1 mm, yellow; disc not seen; ovary c. 1.1 mm diam, glabrous, style 0.3–0.5 mm long, stigmas 0.6–1 mm long, apically shortly bifid, free arms 0.15–0.4 mm long. *Fruits* 0.95–1.2 cm diam, glabrous; pedicel 1.8–3.4 cm long, 1.7–2 mm diam; sepals persistent but not much accrescent; wall 0.5–0.6 mm thick, exocarp partly detaching; columella 6.5–8.7 mm long. *Seeds* 6–7.5 mm diam, reddish brown; hilum rhombic, 1–2 by 0.5–0.6 mm.

Distribution — New Caledonia (endemic).

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

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

7. ***Trigonostemon diplopetalus*** Thwaites — sect. ***Pycnanthera*** — Map 24

Trigonostemon diplopetalus Thwaites, Enum. Pl. Zeyl. (1861) 277; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1108; Hook.f., Fl. Brit. India 5 (1887) 398; Trimen, Handb. Fl. Ceylon 4 (1898) 51, pl. 83; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 93, f. 39; N.P.Balakr. & Chakrab., Candollea 46 (1991) 613, f. 3; Philcox in Dassan., Revis. Handb. Fl. Ceylon 11 (1997) 110. — Lectotype (designated here): *Thwaites CP 578* (lecto G*, barcode G00435106; isolecto A, barcode A00048867, BR*, barcode BR0000005105045, CAL, barcodes CAL0000023676, CAL0000023677, FR*, barcode FR0036073, G*, no barcode, in the same folder with lectotype; G-DC*, barcode G00319791, on 2 sheets, GH*, barcode GH00048868, P, barcode P00717097, P, barcode P00717098, K, barcode K000246865), Sri Lanka.

Map 24 Distribution of *Trigonostemon diplopetalus* Thwaites (●) and *T. nemoralis* Thwaites (▲).

Shrubs or small trees; flowering branches 2–2.8 mm thick, pubescent when young, glabrous in older parts. *Outer bark* 0.1–0.2 mm diam, dark to pale brown; inner bark 0.1–0.3 mm thick; wood pale yellow. *Stipules* subulate, 0.4–1 mm long, caducous, pubescent at base. *Leaves*: petiole terete but grooved above, 0.5–1.2 cm long, 1–1.7 mm diam, slightly pubescent when young; blade oblong to oblanceolate, 14–23.5 by 3.5–5.5 cm, thick chartaceous, lower part cuneately narrowed, decurrent into petiole, 2 adaxial glands present, falcate, margin distantly serrate, teeth falcate, apex acuminate, both surfaces glabrous, slightly pubescent beneath when young; venation pinnate, midrib almost flat above, elevated beneath, secondary veins 11–16 pairs, bifurcate and connected along margin, tertiary veins reticulate, obscure. *Inflorescences* bisexual, racemose thyrses, terminal; axis 3.3–17 cm long, 1.2–1.7 mm diam, pubescent; bracts lanceolate, 0.2–1.3 by 0.4–0.7 mm long, pubescent. *Staminate flowers* (bud) 2–2.2 mm diam; pedicel 1.1–2.5 mm long, 0.35–0.4 mm diam, pubescent; sepals lanceolate, 1.3–1.5 by 0.5–0.7 mm, base connate, apex rounded to acute, pubescent outside; petals (Trimen 1898) about as long as sepals, denticulate and crisped, bilobed, red; disc glands 5 (Balakrishnan & Chakrabarty 1991), c. 0.2 by 0.3 mm; stamens (Balakrishnan & Chakrabarty 1991) 3, sessile? (see note 2), connective fleshy, forming a stalk, c. 0.5 mm long. *Pistillate flowers* (bud) 2–2.1 mm diam; pedicel 5.2–6 mm long, apically 0.5–0.7 mm diam, pubescent; sepals lanceolate to oblong, 2–2.6 by 0.7–1 mm, apex acuminate, pubescent and gibbose (with a horn-like appendage) outside (Balakrishnan & Chakrabarty 1991); petals (Trimen 1898) as in staminate flowers, but larger and reflexed; ovary (Philcox 1997) pubescent, stigma (Trimen 1898) apically twice bifid, with short stout branches. *Fruits* (Philcox 1997) 1–1.5 cm diam, subglobose. *Seeds* (Philcox 1997) 5.5–6 mm diam, pale brown, with shallow longitudinal ridge.

Distribution — Sri Lanka (endemic).

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

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

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

8. ***Trigonostemon eberhardtii*** Gagnep. — sect. ***Tylosepalum*** — Figure 30; Map 25

Trigonostemon eberhardtii Gagnep., Bull. Soc. Bot. France 69 (1922) 749; in Lecomte, Fl. Indo-Chine 5 (1925b) 313. — Lectotype (designated here): *Bon 5239* (lecto P, barcode P00717103), Vietnam, Annam, Thanh-hoa. — Other syntypes: *Eberhardt 4293* (P, barcodes P00717101, P00717102), Vietnam, Tonkin, Hoa-binh, Mai-ha; *Bon 5465* (P, barcodes P00717099, P00717100), Vietnam, Annam, Son-thôn.

Trigonostemon harmandii Gagnep., Bull. Soc. Bot. France 69 (1922) 750; in Lecomte, Fl. Indo-Chine 5 (1925b) 313. — Type: *Harmand 2956* (P, barcodes P00648665, P00648666, P00648667), Cambodia.

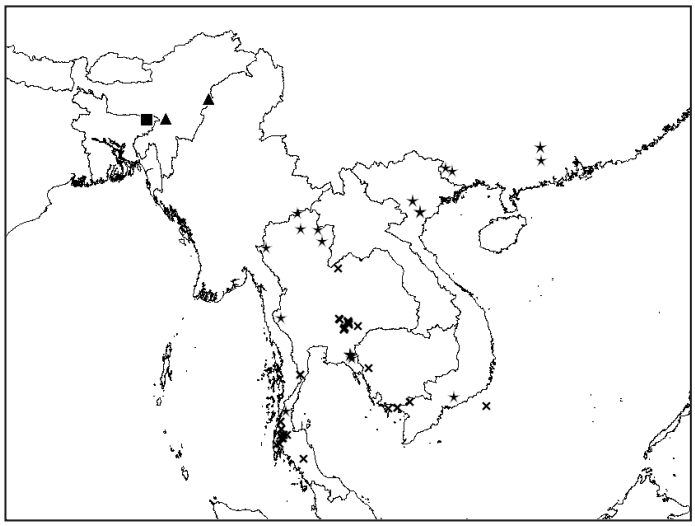
Trigonostemon poilanei Gagnep., Bull. Soc. Bot. France 69 (1922) 753; in Lecomte, Fl. Indo-Chine 5 (1925b) 314, *syn. nov*. — Type: *Poilane 40807* (A, barcode A00048878, P, barcode P00717127), Vietnam, Bienhoa, Giaray.

Trigonostemon albiflorus Airy Shaw, Kew Bull. 25 (1971) 547; Kew Bull. 26 (1972a) 345; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 23; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 574, f. 92. — *Trigonostemon leucanthus* Airy Shaw var. *siamensis* H.S.Kiu in H.S.Kiu & X.X.Chen, Guihaia 12 (1992) 211. — Type: *Winit 1704* (holo K, on 2 sheets, barcodes K000959303, K000959304; iso BK, barcode BK257891, BM, barcode BM000951503), Thailand, Lampang, Mê Pêng.

Trigonostemon leucanthus Airy Shaw, Kew Bull. 25 (1971) 548; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 164. — Type: *Morse 668* (K, barcodes K000959336, K000959337), China, Guangxi, Longzhou.

Trigonostemon wui H.S.Kiu, J. Trop. & Subtrop. Bot. 3 (1995) 19–20, f. 2. — Type: *Kiu* [*H.X. Qiu*] *451* (holo IBSC, not found; iso IBK barcode IBK00190788), China, Guangdong, Fengkai, Yulao.

Shrubs or small trees, 1–5(–7) m tall, dbh 2.8–6.3 cm; flowering branches 1.1–5 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts (and sometimes petals). *Outer bark* c. 0.1 mm thick, dark to



Map 25 Distribution of *Trigonostemon eberhardtii* Gagnep. (⋆), *T. montanus* R.Y.Yu & Welzen (▲) and *T. praetervisus* Airy Shaw (■), *T. quocensis* Gagnep. (×).


a
b
c
d
e
f
g
h

pale brown or greyish brown; inner bark 0.1–0.2 mm thick, brown to reddish brown; wood white to pale yellowish. *Stipules* subulate, 0.3–0.7 mm long, caducous, often pubescent. *Leaves*: petiole terete, grooved or flat above, 0.5–8 cm long, 0.7–2.1 mm diam, glabrous or pubescent; blade elliptic, 8.5–26 by 2.5–8 cm, chartaceous, base acute, 2 adaxial glands present, occasionally sparsely pubescent, margin entire or very distantly serrate, apex acuminate to caudate, upper surface glabrous, dark green, lower surface often very sparsely pubescent, pale green; venation triplinerved, midrib (and sometimes 2 basal secondary veins) slightly raised above and distinctively elevated beneath, pubescent on lower surface, especially near base, other secondary veins 4–7(–10) pairs, bow-shaped and connected along margin, tertiary veins scalariform, veinlets reticulate. *Inflorescences* bisexual, terminal or axillary, paniculate, pistillate flowers open before staminate ones; main axis terete, up to 31.5 cm long, 0.4–2.7 mm diam, pubescent to glabrous; bracts linear to lanceolate to triangular, 0.7–2.7 by 0.3–0.6 mm, pubescent outside, bracteoles linear to lanceolate, 0.4–0.7 by 0.1–0.2 mm, densely pubescent. *Staminate flowers* 6–8 mm diam; buds conical; pedicel 2–9.5 mm long, 0.15–0.3 mm diam, glabrous, light green; sepals elliptic, 1–2.3 by 0.5–0.7 mm, light green, base connate, margin entire, apex acute, often with a short notch and an adaxial gland, pubescent outside; petals obovate, 2.8–5 by 1.5–3 mm, contort, membranous, white, lower part cuneately narrowed, apex rounded, glabrous; disc annular, yellow, margin undulate, often deeply notched, 0.4 (inner margin)–0.6 mm (outer margin) diam; stamens 3, androphore 0.9–1.2 mm long, 0.1–0.2 mm diam, white, filament free part c. 0.2 mm long, white, anthers free, globose to ellipsoid, 0.3–0.4 mm long, yellow. *Pistillate flowers* 6–9 mm diam; buds conical; pedicel slightly thickened toward apex, 3–15.5 mm long, apically 0.45–1.1 mm diam when flowering, glabrescent; sepals as staminate flowers but larger, 1.3–3.8 by 0.6–1.3 mm, apex often with an adaxial gland but without notch; petals as staminate flowers; disc lobes 5, rectangular, 0.3–0.45 by 0.3–0.4 mm, yellow, apex truncate; ovary 1–1.1 mm diam, glabrous, green, style 0.1–0.2 mm long, stigmas 0.8–1.1 mm long, bent, white, apically slightly thickened and slightly bifid. *Fruits*1.1–1.5 cm diam, greenish, glabrous; pedicel 1.9–3.4 cm long, 1.2–1.8 mm diam; sepals persistent but not accrescent; wall 0.4–0.5 mm thick, exocarp partly detaching; columella 4.5–6.5 mm long. *Seeds* 7–8 mm diam, marbled; hilum rhombic, 2.5–3 by 1–2 mm.

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

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

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

2. The species resembles *T*. *viridissimus* (Kurz) Airy Shaw, with which the morphological boundary is sometimes unclear. However, the molecular phylogeny (Yu et al. 2019b) shows that the two species are placed in different subclades within sect. *Tylosepalum* (Kurz) Benth. Main characters that can be used in identification include (1) the white petals (yellow to orange in *T*. *viridissimus*), (2) monopodial branching in the inflorescences with relatively more condensed

Figure 30 *Trigonostemon eberhardtii* Gagnep., private collection of Hua-Shing Kiu, originally from Yulao, Fengkai, Guangdong, China. a. Growing habit; b. leaf base, showing glands; c. staminate flower, top view; d. flower buds and a staminate flower, lateral view; e. pistillate flower; f. fruit; g. inflorescence; h. infructescence. — Photos by Ren-Yong Yu.

staminate flowers (vs. sympodial branching and relatively loose panicles in *T. viridissimus* var. *viridissimus*) and (3) an indistinctive style (shorter than 2 mm in *T. eberhardtii*; up to 6 mm in *T. viridissimus*).

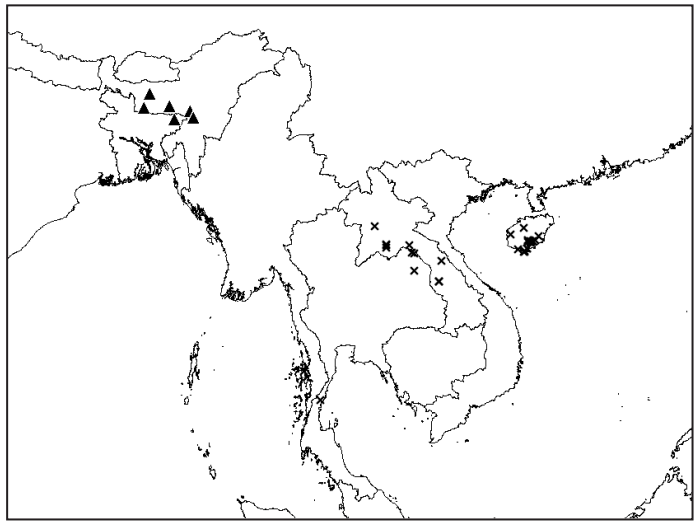
9. ***Trigonostemon flavidus*** Gagnep. — sect. ***Trigonostemon*** — Figure 31; Map 26

Trigonostemon flavidus Gagnep., Bull. Soc. Bot. France 69 (1922) 749; in Lecomte, Fl. Indo-Chine 5 (1925b) 320; P.T.Li & M.G.Gilbert in C.Y.Wu, P.H.Raven & D.Y.Hong, Fl. China 11 (2008) 273; R.Y.Yu & Welzen, Blumea 62 (2018) 195. — Lectotype (designated here): *Harmand 3273* (lecto P, barcode P00717104; isolecto P, barcode P00717105), Laos, in Lakhon mountains, near Me-Kong.

Trigonostemon heterophyllus Merr., Lingnan Sci. J. 9 (1930) 38; N.P.Balakr. & Chakrab., Candollea 46 (1991) 617, f. 5; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 163; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 24; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 577, pl. 31: 1. — Type: *Tsang 594* [*17343*] (A*, barcodes A00048861, A00048862, B*, barcode B100249526, BM, barcode BM000951501, BO, sheet no. BO1695956, CAL, barcode CAL0000023662, ECON*, barcode ECON00254237, G, barcode G00435104, K, barcode K000959339, L, barcode L0160156, MO*, barcode MO-260398, NTUF*, NY*, barcode NY00273341, P, barcode P00717108, PE, barcodes, PE00022683, PE00022684, UC*, barcode UC373861, US*, barcodes US00096533, US00997745, W*, sheet no. W1940-0006789, WIS*, barcode WISv0255641); China, Hainan, Taam Chau District [= Danzhou County], Sha Po Shan [= Mt. Sha Bao].

Trigonostemon sunirmalii Chakrab. & N.P.Balakr., J. Econ. Taxon. Bot. 5 (1984b) 179. — Type: *Biswas 22* (holo CAL, barcode CAL0000023663; iso CAL, barcode CAL0000023664), Myanmar, Tenasserim [= Tanintharyi Region], Nimchaung.

Small trees, 1–2.5 m tall; flowering branches up to 4.5 mm diam, densely pubescent. *Outer bark* 0.1–0.2 mm thick, pale brown to dark grey, smooth or roughened; inner bark 0.1–0.2 mm thick, reddish brown; wood pale yellow. *Stipules* subulate, 0.7–1 mm long, pubescent at base. *Leaves*: petiole terete but sometimes flattened or grooved above, 0.2–1.2 cm long,



Map 26 Distribution of *Trigonostemon flavidus* Gagnep. (×); *T. semperflorens* (Roxb.) Müll.Arg. (▲).

0.7–2.4 mm diam, densely pubescent; blade obovate or oblanceolate, cuneately narrowed and sometimes unequal in the lower middle part, 9–35 by 5–9 cm, chartaceous, base abruptly rounded to truncate, with 2 adaxial glands, margin distantly serrate, teeth small and nipple-like, apex caudate to acuminate, upper surface dark to light green, lower surface paler, both surfaces pubescent, especially on secondary veins and margin; venation pinnate; midrib thin, elevated on both surfaces, secondary veins 10–13 pairs, tertiary veins reticulate, often obscure. *Inflorescences* bisexual, in short cymes or thyrses, cauliflorous or supported by a peduncle and involucral bracts; peduncle 1–9 cm long, pubescent; involucral bracts lanceolate, 8–38 by 0.7–9 mm, pubescent; bracts lanceolate to linear, 1.1–5.5(–15) by 0.2–0.7(–2) mm pubescent. *Staminate flowers* 3.6–6 mm diam; pedicel 2.4–4.7 mm long, 0.15–0.3 mm thick, pink to light green, glabrous; sepals elliptic or obovate, 1.1–2.4 by 0.5–1.8 mm, green, base connate, margin ciliate, apex often acute to rounded, occasionally with a notch, pubescent outside; petals obovate, 2.1–4.2 by 1.7–2.2 mm, base claw-like, apex rounded, glabrous, dark reddish to maroon-purple to black; disc lobes obovate or rectangular, 0.4–0.7 by 0.15–0.25 mm, sometimes narrowed at base, often reflected at apex, light orange, glabrous; stamens 3, androphore 1–1.2 mm long, c. 0.1 mm diam, white, shortly trifid at apex, filament free parts 0.1–0.2 mm long; anthers free, divaricate at apex, thecae 0.4–0.6 mm long, pale yellow, connective pinkish red, with numerous droplets with secretion. *Pistillate flowers* few, slightly enlarged when fruiting, up to c. 1 cm diam; pedicel c. 1.5 mm long and c. 0.5 mm diam in flower bud, accrescent to c. 7 mm long and apically c. 1 mm diam when fruiting; sepals lanceolate to linear, 2.2–3.4 by 1–1.5 mm when flowering, accrescent to 2.4 by 0.9 cm in fruit, margin entire or with a few teeth, apex acuminate, pubescent outside; petals elliptic, 3–3.3 by 2–2.7 mm (flower bud), caducous; disc glands rectangular to semi-orbicular, 0.5–0.6 by 0.4–0.6 mm, rounded or truncate at apex, glabrous; ovary c. 0.7 mm diam, bright dark green, densely pubescent, styles almost indistinct, stigmas 3, completely divided, free arms 0.6–0.7 mm long. *Fruits* c. 1.2 cm diam, green when young, brown when mature, densely pubescent; wall woody, 0.5–0.55 mm thick; columella 4.2–6.7 mm long. *Seeds* 4.2–6.7 by 4.5–5.7 mm, light or dark brownish when dry, hilum irregularly shaped, more or less triangular, 0.8–1.3 by 0.5–0.7 mm diam.

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

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

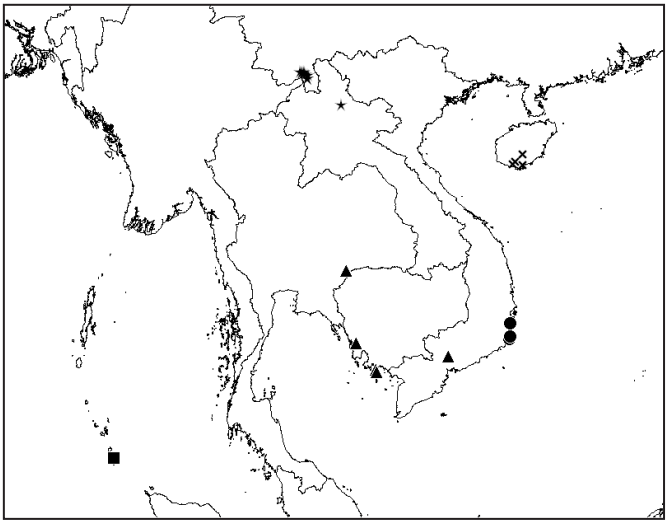
Note — *Trigonostemon flavidus* strongly resembles *T. semperflorens* (Roxb.) Müll.Arg. from India but has much denser and stronger hairs (Yu & Welzen 2018, Balakrishnan & Chakrabarty 1991). We treat them as separate species, because there is a clear gap in the extent of pubescence (pubescent in *T.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

10. ***Trigonostemon fragilis*** (Gagnep.) Airy Shaw — sect. ***Tylosepalum*** — Map 27

Trigonostemon fragilis (Gagnep.) Airy Shaw, Kew Bull. 32 (1978) 415. — *Poilaniella fragilis* Gagnep., Bull. Soc. Bot. France 72 (1925a) 467; in Lecomte, Fl. Indo-Chine 5 (1925b) 307. — Lectotype (designated here): *Poilane 2927* (lecto P, barcode P00712172; isolecto A, barcode A00106974, not seen, P, barcodes P00712173, P00712174), Vietnam, Annam, Tre Island, near Nhatrang.

Shrubs, 2–3 m tall; flowering branches 1.1–2.5 mm diam, pubescent when young, glabrous in old parts. *Outer bark* 0.1–0.2 mm thick, pale brown to grey; inner bark 0.1–0.3 mm thick, pale to

Figure 31 *Trigonostemon flavidus* Gagnep., cultivated in South China Botanical Garden. a. Growing habit; b. bark; c. cauliflorous staminate inflorescences; d. staminate flowers, lateral view; e. staminate flower, top view;



Map 27 Distribution of *Trigonostemon fragilis* (Gagnep.) Airy Shaw (●), *T. lii* Y.T.Chang (★), *T. murtonii* Craib (▲), *T. villosus* Hook.f. var. *nicobaricus* (Chakrab.) N.P.Balakr. & Chakrab. (■) and *T. xyphyphylloides* (Croizat) L.K.Dai & T.L.Wu (✕).

reddish brown; wood pale yellowish to brown. *Stipules* subulate, 0.2–0.5 mm long, caducous, often indistinct, pubescent at base. *Leaves*: petiole terete, grooved above, 0.5–2.4 cm long, 0.5–1 mm diam, glabrescent; blade elliptic to ovate, 1.8–5.5 by 1.2–3 cm, chartaceous, base acute to rounded or sometimes truncate, 2 adaxial glands present, margin entire, apex acute or rounded, both surfaces glabrescent, particularly pubescent within the axils of midrib and lateral veins and one or more domatia sometimes present; venation triplinerved, midrib and basal secondary veins flat or slightly raised above and elevated beneath, other secondary veins 3–4 pairs, curved and connected along margin, tertiary veins reticulate, often obscure. *Inflorescences* seemingly unisexual, terminal or axillary, cymes or thyrses; axis terete, 1–3.8 cm long, 0.4–0.7 mm diam, glabrescent; bracts lanceolate to oblong, 0.2–1 by 0.2–0.5 mm, pubescent outside. *Staminate flowers* (bud) c. 2.4 mm diam; pedicel 6.4–7.5 mm long, slightly thickening toward apex, 0.3–0.7 mm diam, slightly pubescent; sepals elliptic, unequal, 1.2–2.1 by 0.9–1.5 mm, margin entire, apex rounded, pubescent outside; petals flabellate, but elliptic when young, 1.5–1.6 by 1–1.4 mm, apex sometimes slightly bilobed; disc annular, c. 0.2 mm wide; stamens 3, androphore erect, c. 0.1 mm long, anthers ellipsoid, 0.8–0.9 mm long. *Pistillate flowers* (flattened) c. 1 cm diam; pedicel slightly thickened toward apex, 7.3–10 mm long, apically 0.5–0.7 mm diam; sepals elliptic, 1.6–3.2 by 0.9–1.4 mm, margin entire, apex acute, pubescent outside; petals flabellate, 3.2–5 by 3.2–5.4 mm, apex slightly bilobed; disc annular, 0.2–0.3 mm wide; ovary 0.7–1 mm diam, glabrous, style absent, stigmas 0.4–0.55 mm long, thickened and with a very shallow groove at apex. *Fruits* 1.2–1.3 cm diam, glabrous; wall 0.7–1 mm thick, exocarp 0.3–0.6 mm thick, completely detaching; columella 7.1–7.8 mm long; *Seeds* flattened globose, 10–10.5 by 9–9.5 mm, hilum oblong, 2.3–2.4 by 1.1–1.5 mm.

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

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

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

←

f. staminate flower, back view; g. young pistillate flowers and mature fruit; h. young fruit; i. staminate flower with 4 stamens (abnormal growth). — Photos by Ren-Yong Yu.

11. ***Trigonostemon heteranthus*** Wight — sect. ***Tylosepalum*** — Map 20

Trigonostemon heteranthus Wight, Icon. Pl. Ind. Orient. 5 (1852) 24, t. 1890; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1109; Kurz, Forest Fl. Burma 2 (1877b) 406 ('*heteranthum*'); Hook.f., Fl. Brit. India 5 (1887) 396; N.P.Balakr. & Chakrab., Candollea 46 (1991) 615, f. 4. — Lectotype (designated here): *Griffith KD 4796* (lecto K, barcode K000246910; isolecto P, barcode P00717107). Myanmar, Mergui. — Other syntypes: *Griffith s.n*. (K, barcode K000246861); Myanmar, Mergui, *Helfer KD 4796* (K, barcode K000246862), Myanmar, Mergui.

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

Distribution — Myanmar (Mergui and Tavoy, endemic).

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

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

12. ***Trigonostemon inopinatus*** Airy Shaw — sect. ***Spinipollen*** — Map 23

Trigonostemon inopinatus Airy Shaw, Kew Bull. 31 (1976) 396; Kew Bull. 35 (1980a) 691. — Type: *Webb & Tracey 7762* (holo BRI, barcode BRI-AQ0205473, on 2 sheets), Australia, Queensland, Cawley State Forest, west of Cathu between Mackay & Proserpine.

Small trees or shrubs, up to 7 m tall; flowering branches 1.1–2.2 mm diam, pubescent when young, glabrous in old parts. *Outer bark* c. 0.1 mm thick, pale brown to grey; inner bark c. 0.1 mm thick, reddish brown; wood pale yellowish. *Stipules* subulate, 0.1–0.35 mm long, sometimes pubescent at base. *Leaves*: petiole terete, grooved above, 1–2.2 cm long, 0.8–1.7 mm diam,

sometimes very slightly thickened towards base and apex, pubescent; blade elliptic, 5–10 by 2.4–4.8 cm, chartaceous, base acute, 2 adaxial glands present, margin distantly serrate, apex acute to acuminate, upper surface pubescent when young, glabrescent, lower surface often pubescent; venation pinnate, midrib flat above and elevated beneath, pubescent beneath, secondary veins 4–8 pairs, curved and connected along margin, tertiary veins reticulate, often obscure. *Inflorescences* bisexual, axillary; staminate ones thyrsoid, dichotomously branching, often subtended by bracts and supported by a peduncle, peduncle terete, 0.8–4.5 cm long, 0.4–1 mm diam, pubescent, bracts oblong, 2.8–25 by 1–6 mm, pubescent on both sides; pistillate inflorescences cymes, peduncle terete, 1.2–2.5 cm long, 0.5–1 mm diam, bracts oblong to lanceolate, 7–16 by 2–3.8 mm, pubescent on both sides. *Staminate flowers* c. 6 mm diam; pedicel thickening towards apex, 4.2–6 mm long, apically 0.4–0.6 mm diam, pubescent; sepals elliptic to lanceolate, 1.8–2.7 by 0.7–0.8 mm, base connate, margin entire, apex acuminate, pubescent outside; petals obovate to flabellate, 3–3.5 by 2.1–2.2 mm, yellow or cream, glabrous, with a reddish honey mark near base, apex rounded; disc glands 5, 0.5–0.6 by 0.2–0.3 mm; stamens 3, androphore c. 1.3 mm long, c. 0.4 mm diam, anthers ellipsoid, 0.7–0.8 mm long. *Pistillate flowers* c. 7.5 mm diam; pedicel thickening towards apex, 9.5–13 mm long and apically 1–1.2 mm diam when flowering, elongating to 1.7–2.3 cm long and apically 1.5–1.7 mm diam in fruit, pubescent; sepals lanceolate, 4–7.5 by 1.2–2.2 mm when flowering, enlarged up to 18 by 6.7 mm when fruiting, green, pubescent on both sides, base connate, margin entire, apex acuminate; petals as in staminate flowers, but larger and caducous, 4–5 by 3.5–4.8 mm; disc annular, 5-notched, membranous; ovary c. 1.6 mm diam, pubescent; style absent; stigmas 0.9–1 mm long, in middle c. 0.5 mm diam, adaxially grooved, apically thickened and horseshoe-like, 0.8–0.9 mm diam. *Fruits* sparsely pubescent; sepals persistent; wall 0.4–0.5 mm thick, exocarp partly detaching; columella 5.5–6.5 mm long. *Seeds* 6.7–7 mm diam, brown; hilum round, 1.7–1.8 by 1–1.5 mm.

Distribution — Australia (Queensland, endemic).

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

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

13. ***Trigonostemon kerrii*** Craib — sect. ***Trigonostemon*** — Map 20

Trigonostemon kerrii Craib, Bull. Misc. Inform., Kew (1924) 97; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1925b) 321; Airy Shaw, Kew Bull. 26 (1972a) 346; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 25; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 577. — Lectotype (designated by Chantaranothai 2005): *Kerr 5871* (lecto BK*, barcode BK239811, isolecto A*, barcode A00048870, P, barcode P04810877), Thailand, Nakawn Tai.

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

3.6 by 0.2–0.9 mm, pubescent. *Staminate flowers* c. 2.8 mm diam; pedicel 2.5–6 mm long, 0.1–0.2 mm diam, glabrescent; sepals elliptic to lanceolate, 0.9–1.5 by 0.5–0.9 mm, base connate, margin often serrate, apex acuminate to rounded, pubescent outside; petals in flower bud elliptic, 1.1–1.4 by 0.7–0.9 mm, apex rounded, purplish red (Craib 1924); disc glands 5, c. 0.15 by 0.1 mm; stamens 3, androphore indistinct (flower too young), anthers ellipsoid, 0.7–0.8 mm long. *Pistillate flowers* (bud) c. 1.7 mm diam; pedicel c. 2.6 mm long, 0.4–0.5 mm diam, glabrescent; sepals triangular, 1.6–1.9 by 0.7–0.9 mm, base connate, margin fringed with capitate glands, apex acuminate; petals elliptic, 1.7–2.2 by 1–1.3 mm, apex rounded, purplish red (Craib 1924); disc glands 5, c. 0.2 by 0.2 mm; ovary c. 0.7 mm diam, glabrous, style absent, stigmas c. 0.25 mm long, apically seemingly bifid. *Fruits* glabrous; pedicel c. 1.8 cm long, c. 0.7 mm diam, glabrescent; sepals accrescent, persistent, lanceolate, 5–6 by 1.5–2 mm, margin fringed with capitate glands; wall 0.3–0.4 mm thick, exocarp not detaching; columella c. 3 mm long. *Seeds* not seen.

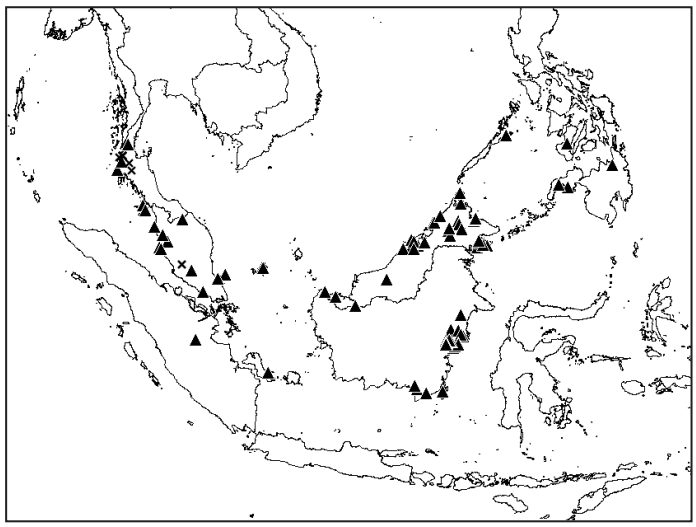
Distribution — Thailand and Cambodia (Kampong Thom).

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

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

14. ***Trigonostemon laevigatus*** Müll.Arg. — sect. ***Tylosepalum*** — Map 28

Trigonostemon laevigatus Müll.Arg., Flora 47 (1864b) 538; in A.DC., Prodr. 15, 2 (1866) 1111; Boerl., Handl. Fl. Ned. Ind. 1 (1900) 232, 284; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 94; Merr., J. Straits Branch Roy. Asiat. Soc., Spec. No. (1921) 345 (2nd mentioning, first = *Microdesmis caseariifolia* Planch., see Jablonski, 1963: 168); Ridl., Fl. Malay Penins. 3 (1924) 265; Jabl., Brittonia 15 (1963) 167; Airy Shaw, Kew Bull. 26 (1972a) 346; Whitmore, Tree Fl. Malaya 2 (1973) 135; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 203; Kew Bull. 32 (1978) 417; Kew Bull. 36 (1981) 355; Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 25; in Welzen & Chayam. in Santisuk & K.Larsen,



Map 28 Distribution of *Trigonostemon laevigatus* Müll.Arg. var. *laevigatus* (▲) and *T. laevigatus* var. *croceus* (B.C.Stone) R.Y.Yu & Welzen (×).

Fl. Thailand 8, 2 (2007) 578, f. 93; R.Y.Yu & Welzen, Blumea 62 (2018) 195, f. 5. — Lectotype (designated by Yu & van Welzen 2018): *Motley 686* (lecto K, barcode K000959291), Borneo, South Kalimantan, Bangarmassing [= Banjarmasin].

Description and taxonomic notes see Yu & van Welzen 2018.

Key to the varieties

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

a. var. ***laevigatus*** — Map 28

Description and taxonomic notes see Yu & van Welzen 2018.
Distribution — Vietnam?, Thailand, Malay Peninsula, Sumatra, Java, Borneo, Philippines.

b. var. ***croceus*** (B.C.Stone) R.Y.Yu & Welzen — Map 28

Trigonostemon laevigatus Müll.Arg. var. *croceus* (B.C.Stone) R.Y.Yu & Welzen, Blumea 62 (2018) 197. — *Trigonostemon croceus* B.C.Stone (1980) 289. — Type: *Stone 9586* (holo KLU, sheet no. 13345; iso K, L, barcode L.2258563), Malaysia, Selangor, on the Pahang border at Genting Sempah.

Description and taxonomic notes see Yu & van Welzen 2018.
Distribution — Thailand (Surat Thani, Phangnga, Ranong) and Malay Peninsular (Selangor).

15. ***Trigonostemon lanceolatus*** (S.Moore) Pax — sect. ***Trigonostemon*** — Map 22

Trigonostemon lanceolatus (S.Moore) Pax in Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 92. — *Nepenthandra lanceolata* S.Moore, J. Bot. 43 (1905) 149, pl. 471, f. 7–13. — Type: *Beddome s.n*. (BM, barcode BM000951502), Myanmar, Tenasserim [= Tanintharyi Region], Mooleyit slopes.
Trigonostemon phyllocalyx Gagnep., Bull. Soc. Bot. France 72 (1925a) 469; in Lecomte, Fl. Indo-Chine 5 (1925b) 312; Airy Shaw, Kew Bull. 26 (1972a) 348; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 27; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 581, *syn*. *nov*. — Type: *Poilane 2700* (A, barcode A00048879, P, barcodes P00717119, P00717120), Vietnam, Annam, Nhatrang.

Trees, to 5 m tall, dbh to 5 cm; flowering branches 1.9–3.5 mm diam, pubescent when young, glabrous in old parts. *Outer bark* 0.1–0.2 mm thick, brown to pale or greyish brown; inner bark 0.1–0.2 mm thick, reddish brown, sap red; wood yellow to brown. *Stipules* subulate, 0.4–1.1 mm long, caducous, pubescent at base. *Leaves*: petiole terete, grooved above, 1.4–11.5 cm long, 0.8–2 mm diam, hirsute to glabrous; blade lanceolate to oblong, 6.8–21 by 2.3–8.2 cm, thick-chartaceous, base acute to rounded, 2 adaxial glands present, margin distantly serrate, apex acuminate to slightly caudate, both surfaces glabrous; venation pinnate, midrib flat or slightly raised above and elevated beneath, sometimes slightly pubescent beneath, secondary veins 6–10 pairs, curved, connected along margin, tertiary veins and veinlets reticulate. *Inflorescences* bisexual, often axillary, racemose thyrses, pistillate flowers open first, single per node near apex of axis, staminate flowers usually 1–3 per node below; axis up to 8.7 cm long, 0.5–0.8 mm diam, hirsute to glabrescent, bracts oblong, 0.4–6.5 by 0.1–1.4 mm, pubescent.

Staminate flowers (bud) c. 2.4 mm diam; pedicel thickening toward apex, 1.8–2.5 mm long, apically 0.4–0.8 mm diam, slightly hirsute; sepals ovate to elliptic, 1.2–1.9 by 0.8–1.5 mm, base connate, margin entire, sometimes ciliate, apex rounded to acute, pubescent or hirsute outside; petals ovate to elliptic, 1.1–1.4 by 0.9–1.15 mm diam, glabrous, apex rounded; disc annular, c. 0.1 mm wide, ring c. 0.8 mm diam; stamens 3, androphore c. 0.1 mm long, anthers ellipsoid, 0.5–0.7 mm long, divaricate. *Pistillate flowers* 5–10 mm diam; pedicel thickening towards apex, 3–7 mm long, apically 1–1.2 mm diam, pubescent or hirsute; sepals triangular, 4–5.5 by 2.7–3 mm when flowering, significantly accrescent, up to 1.3 by 1.1 cm when fruiting, densely hirsute on both sides, base connate, margin mostly entire but with two teeth near apex, apex acuminate; petals elliptic, 2.5–3 by 1.8–2.6 mm, apex rounded; disc seemingly annular, c. 0.6 mm wide; ovary c. 1.7 mm diam, glabrous to hirsute; style absent; stigmas deeply bifid, 0.6–0.7 mm long, free arm V-shaped at base. *Fruits* 1–1.1 cm diam, densely hirsute, smooth; sepals persistent; wall 0.3–0.4 mm thick. *Seeds* c. 7.5 mm diam, marbled; hilum triangular, c. 2.5 by 1.7 mm.

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

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

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

16. ***Trigonostemon lii*** Y.T.Chang — sect. ***Tylosepalum*** — Map 27

Trigonostemon lii Y.T.Chang, Guihaia 3 (1983) 175; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 166. — Type: *Li 4576* (holo KUN, barcode KUN1294357), China, Yunnan, Xishuangbanna Botanical Garden.

Shrubs or small trees, 1–4.5 m tall; flowering branches 1.2–2.5 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots absent in green parts. *Outer bark* c. 0.1 mm thick, dark brown to somewhat reddish brown; inner bark c. 0.1 mm thick, reddish brown to dark red; wood pale yellowish. *Stipules* subulate, 0.5–0.8 mm long, caducous, often pubescent. *Leaves*: petiole terete, grooved above, 0.5–2 cm long, 0.9–1.5 mm diam, slightly pubescent when young; blade oblong, 8.5–18 by 2–5.2 cm, coriaceous, base acute, 2 adaxial glands present, margin very distantly serrate, apex acuminate to somewhat caudate, above glabrous, below glabrescent; venation very distinctively triplinerved, midrib slightly raised above and elevated beneath, sometimes slightly pubescent beneath, secondary veins 3–7 pairs, bow-shaped (except for 2 basal secondary veins) and connected along margin, tertiary veins scalariform, veinlets reticulate, obscure. *Inflorescences* bisexual, terminal or axillary, paniculate thyrses, pistillate flowers single per node, staminate flowers often a cyme per node; main axis terete, 6.5–10 cm long, 0.4–1 mm diam, pubescent; bracts linear to lanceolate, 1–7 by 0.2–1 mm, pubescent. *Staminate flowers* 6–7 mm diam; pedicel 4–7 mm long, 0.2–0.3 mm diam, slightly pubescent; sepals elliptic to lanceolate or oblong, 1.1–2.3 by 0.7–1 mm, base connate, margin entire, apex acute to acuminate, pubescent and often with a notch and a gland outside; petals obovate, 2.8–3.5 by 1.5–2 mm, contort, membranous, yellow, apex rounded, glabrous; disc annular, margin undulate, often deeply notched, c. 0.4 mm wide; stamens 3, androphore c. 0.9 mm long, c. 0.2 mm diam, free part of filaments 0.1–0.2 mm long, white, anthers free, ellipsoid, 0.5–0.6 mm long. *Pistillate flowers* 7–13 mm diam; pedicel slightly thickened toward apex, 0.8–1.7 cm long, 0.7–1.1 mm diam, slightly pubescent; sepals lanceolate, 2.2–5 by 0.8–2 mm, apex acuminate, pubescent outside; petals flabellate, 5–8 by 5–6 mm, base cuneately narrowed, somewhat claw-like, apex rounded; disc cupular, c. 0.3 mm wide, margin undulate, with deep notches; ovary c. 0.9 mm diam, glabrous, style c.

0.2 mm long, stigmas 0.8–1.2 mm long, apex slightly thickened and slightly bifid or not. *Fruits* c. 1.3 cm diam, green, glabrous; pedicel 1.7–2.65 cm long, 1–1.5 mm diam; sepals persistent but not accrescent; wall 0.6–0.8 mm thick, exocarp not detaching; columella 4.5–7 mm long. *Seeds* c. 7.5 by 6.5 mm diam; hilum rhombic, c. 1.5 by 1.5 mm.

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

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

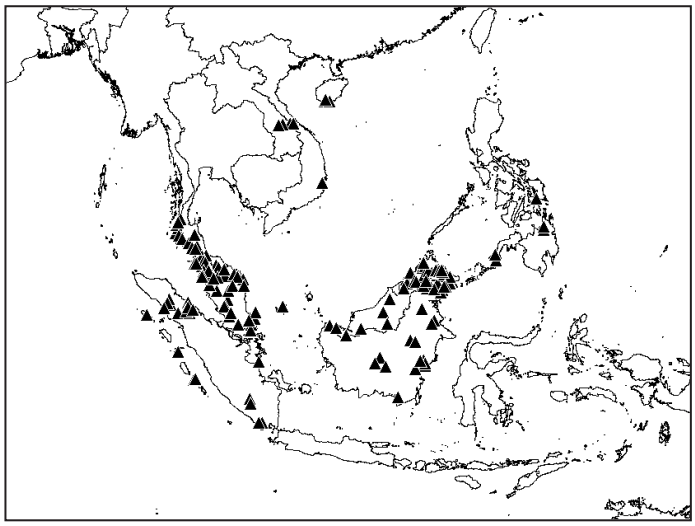
Note — The species can be distinguished from *T. eberhardtii* by the coriaceous, oblong leaves with very distinctive triplinerved venation and lacking oil dots.

17. ***Trigonostemon longifolius*** Wall. ex Baill. — sect. ***Spinipollen*** — Map 29

Trigonostemon longifolius Wall. ex Baill., Étude Gén. Euphorb. Atlas (1858) 23, pl. 11, f. 12 ('*longifolium*'); Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1108; Kurz, Forest Fl. Burma 2 (1877b) 406 ('*longifolium*'); Hook.f., Fl. Brit. India 5 (1887) 396; Pax & K.Hoffm. in Engl., Pflanzenfam. IV.147.iii (1911) 88, f. 28; Ridl., Fl. Malay Penins. 3 (1924) 264; Jabl., Brittonia 15 (1963) 162; Airy Shaw, Kew Bull. 26 (1972a) 347; Whitmore, Tree Fl. Malaya 2 (1973) 136; Airy Shaw, Kew Bull. 36 (1981) 355; N.P.Balakr. & Chakrab., Candollea 46 (1991) 621, f. 7; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 26; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 579, f. 94; R.Y.Yu & Welzen, Blumea 62 (2018) 197, f. 6. — [*Croton longifolius* Wall., Numer. List (1847) nr. 7717 ('*longifolium*'), nom. nud., non Müll.Arg., Fl. Bras. 11 (1873) 170]. — Lectotype (designated by Yu & van Welzen 2018): *Wallich 7717* (lecto K, barcode K000959328; isolecto G, K, barcode K000959327), Malay Peninsula, Penang Island.

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

?Athroisma serratum Griff., Notul. 4 (1854a) 477 ('*serratis*'); Ic. Pl. Asiat. 4 (1854b) pl. 585, f. 9. — Type: *Griffith s.n.*? (K?), Myanmar, Mergui, Tenasserim [= Tanintharyi Region] (see Airy Shaw 1972a: 347).



Map 29 Distribution of *Trigonostemon longifolius* Wall. ex Baill.

Prosartema gaudichaudii Gagnep., Bull. Soc. Bot. France 72 (1925a) 468, non *Trigonostemon gaudichaudii* (Baill.) Müll.Arg., Linnaea 34 (1865) 213. — *Trigonostemon gagnepainianus* Airy Shaw, Kew Bull. 32 (1978) 415. —Syntypes: *Gaudichaud 167* (P, barcodes P00717170, P00712171), Vietnam, Tourane; *Poilane 8306* (P, barcode P00717169), Vietnam, km 26 from Nhatrang to Ninh Hoa; *10220* (NY, barcode NY00273185, P, barcodes P00717158, P00717159), Vietnam, Quang Tri, Dent du Tigre; *Poilane 10446* (K, P, barcodes P00717166, P00717167, P00717168), Vietnam, Quang Tri, Mai Lanh.

Trigonostemon howii Merr. & Chun, Sunyatsenia 2 (1935) 262; H.S.Kiu, Fl. Republ. Popul. Sin. 44(2) (1996) 163. — Type: *How 70940* (A, barcode A00048863, IBK, barcode IBK00169510, K, barcode K000959338, KUN, barcode KUN0403446, NY, barcode NY00273342, PE, barcode PE01110915, US, barcode US00096534), China, Hainan, Yaichow [= Yazhou], Licai [according to the duplicate in IBK] or Luopeng [according to the duplicates in KUN and PE].

Trigonostemon honbaensis Tagane & Yahara, Acta Phytotax. Geobot. 68 (2017) 39, *syn. nov*. — Type: *Toyama*, *Dang*, *Tagane*, *Fuse*, *Yahara*, *Nagamasu*, *Tran*, *Nguyen*, *Nguyen*, *Do*, *Ho V1345* (holo KYO*; iso FU, not seen, VNM, not seen, the herbarium of Hon Ba Nature Reserve, not seen), Vietnam, Khanh Hoa Province, Mt. Hon Ba.

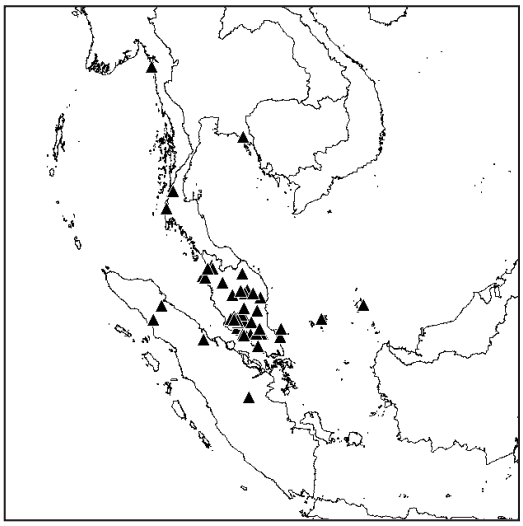
Description see Yu & van Welzen 2018.

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

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

18. ***Trigonostemon malaccanus*** Müll.Arg. — sect. ***Trigonostemon*** — Map 30

Trigonostemon malaccanus Müll.Arg., Flora 47 (1864a) 482; in A.DC., Prodr. 15, 2 (1866) 1110; Hook.f., Fl. Brit. India 5 (1887) 396; Pax & K.Hoffm. in Engl., Pflanzenfam. IV.147.iii



Map 30 Distribution of *Trigonostemon malaccanus* Müll.Arg.

(1911) 90; Ridl., Fl. Malay Penins. 3 (1924) 265; Jabl., Brittonia 15 (1963) 154; Whitmore, Fl. Malay Penins. 2 (1973) 136; Airy Shaw, Kew Bull. 36 (1981) 355; R.Y.Yu & Welzen, Blumea 62 (2018) 201, f. 8. — Type: *Griffith KD 4782* (K, barcode K000959325), Malay Peninsula, Malacca.

Trigonostemon laetus Baill. [Étude Euphorb. (1858) 341 ('*laetum*'), nom. nud.] ex Müll.Arg., in A.DC., Prodr. 15(2) (1866) 1109; Kurz, Forest Fl. Burma 2 (1877b) 407; Hook.f., Fl. Brit. India 5 (1887) 397; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 90; N.P.Balakr. & Chakrab., Candollea 46 (1991) 619, f. 6, *syn*. *nov*. — Syntypes: *Wallich 7740B* (G-DC, barcodes G00319769, G00319757, on 3 sheets, P, barcodes P00717111, P00717112; isosyn CAL, barcode CAL0000023673), Myanmar, Amherst.

Description see Yu & van Welzen 2018.

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

Note — The name *Trigonostemon laetus* was referred to by Baillon (1858) without any description. It was validated by Müller (1866), later than Müller´s (1864a) description of *T. malaccanus* Müll.Arg.

19. ***Trigonostemon montanus*** R.Y.Yu & Welzen, *sp. nov*. — sect. ***Tylosepalum*** — Figure 32; Map 25

Trigonostemon montanus R.Y.Yu & Welzen resembles *T. lii* Y.T.Chang in the oblong leaves, which remain green when dry, but differs in having shorter and dichotomously branching inflorescences. — Type: *Koelz 27903* (holo L, barcode L.2260526), India, Assam, Cachar, Laikul, 6,000 ft, 6 May 1951. Paratypes: *Koelz 27849* (L, barcode L.2260525), India, Assam, Cachar, Laikul, 4,000 ft, 1 May 1951; *Bor 2783* (K), India, Assam, Naga Hill, 5,000 ft, 26 Apr 1935.

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

Distribution — India (Assam, endemic).

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

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

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

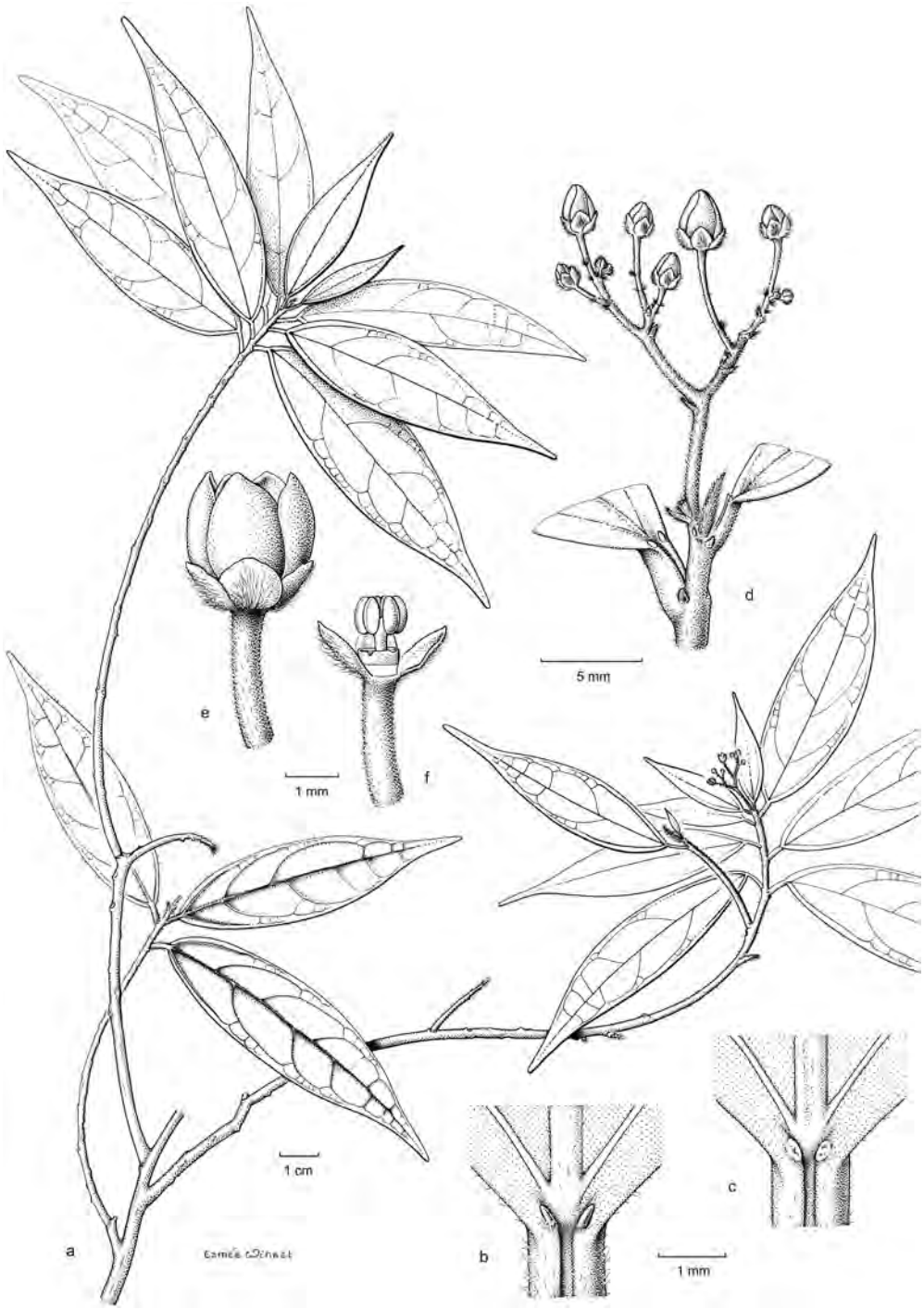


Figure 32 *Trigonostemon montanus* R.Y.Yu & Welzen. a. Growing habit; b. leaf base, showing adaxial glands; c. leaf base, adaxial glands fallen; d. staminate inflorescence; e. staminate flower; f. staminate flower, petals

20. ***Trigonostemon murtonii*** Craib — sect. ***Trigonostemon*** — Map 27

Trigonostemon murtonii Craib, Bull. Misc. Inform., Kew (1911) 464 ('*murtoni*'); Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vi (1912c) 128; Airy Shaw, Kew Bull. 26 (1972a) 347; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 26; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 581. — Type: *Murton 18* (K, barcode K000959311), Thailand, west coast, Koh Klone.

Trigonostemon pierrei Gagnep., Bull. Soc. Bot. France 64 (1922) 752; in Lecomte, Fl. Indo-Chine 5 (1925b) 321, *syn. nov*. — Type: *Pierre 1530* (A*, barcode A00048875, K, barcode K000959307, P, barcodes P00717121, P00717122, P00717123, US*, barcode US00096541), Vietnam, Phu Quoc, Mt. Ong Chao.

Trigonostemon pinnatus Gagnep., Bull. Soc. Bot. France 64 (1922) 752; in Lecomte, Fl. Indo-Chine 5 (1925b) 318. — Type: *Pierre s.n*. (K, barcodes K000959309, K000959310, P, barcodes P00717124, P00717125, P00717126, NY*, US*), Vietnam, Cochinchina, prov. de Bien Hoa, Mt. Lap-vo.

Shrubs, 1–5 m tall; flowering branches 1.1–3.5 mm diam, pubescent when young, glabrous in old parts. *Outer bark* c. 0.1 mm thick, dark brown to pale grey; inner bark c. 0.1 mm thick, reddish brown; wood pale yellowish. *Stipules* subulate, 0.3–0.7 mm long, caducous, often pubescent at base. *Leaves*: petiole terete, grooved above, 0.2–1.9 cm long, 0.7–1.5 mm diam, pubescent; blade oblanceolate to oblong, 5–20 by 1.2–4.3 cm, chartaceous to coriaceous, base rounded to acute, 2 adaxial glands present, margin entire, occasionally with glandular or subulate teeth, apex acuminate to short-caudate, both surfaces glabrous; venation pinnate, midrib elevated on both sides, sometimes furrowed above, often sparsely pubescent beneath, secondary veins 9–18 pairs, curved, bifurcate and connected along margin, tertiary veins reticulate, obscure. *Inflorescences* bisexual, terminal or axillary racemes (flowers clustered at apex) or panicles (spreading like a broom at apex); peduncle up to 7 cm long, 0.3–0.7 mm diam, pubescent; bracts oblong to lanceolate, 1–8.5 by 0.2–1.5 mm, pubescent on both sides. *Staminate flowers* 3–5 mm diam; pedicel 3–4.5 mm long, 0.1–0.2 mm diam, pubescent; sepals elliptic, 0.8–1.5 by 0.5–0.8 mm, base connate, margin entire, apex acuminate, acute, rounded or bilobed, pubescent outside; petals obovate to spathulate, 1.6–2.7 by 1–2 mm diam, dark pink, glabrous, apex rounded; disc glands 5, 0.3–0.35 by 0.1–0.15 mm; stamens 3, androphore c. 0.5 mm long, c. 0.25 mm diam, anthers ellipsoid, 0.4–0.5 mm long, connective with droplets (expanded cells) with secretion. *Pistillate flowers* 3.3–8 mm diam; pedicel thickening towards apex, 3.5–7 mm long, apically 0.5–1 mm diam, elongating to c. 1 cm long in fruit, pubescent; sepals lanceolate, 5–6 by 1–1.6 mm, slightly accrescent to 8 by 2.2 mm when fruiting, pubescent outside, especially along midrib, base connate, margin entire, apex acuminate; petals as in staminate flowers; disc lobes rectangular, 0.2–0.25 by 0.25–0.3 mm, apex truncate; ovary 0.6–1.3 mm diam, densely pubescent; style indistinct, less than 0.1 mm long; stigmas apically deeply bifid, free arms coiled. *Fruits* (young) pubescent. *Seeds* not seen.

Distribution — Thailand, Cambodia and Vietnam.

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

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

←

and 2 sepals removed, showing the androphore and disc (all: *Koelz 27903*, barcode L.2260526). — Drawing by Esmée Winkel, 2019.

21. ***Trigonostemon nemoralis*** Thwaites — sect. ***Pycnanthera*** — Map 24

Trigonostemon nemoralis Thwaites, Enum. Pl. Zeyl. (1861) 277; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1108; Hook.f., Fl. Brit. India 5 (1887) 398; Trimen, Handb. Fl. Ceylon 4 (1898) 51; Bourd., For. Trees Travancore (1908) 504; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 93; Gamble, Fl. Madras (1925) 1341; N.P.Balakr. & Chakrab., Candollea 46 (1991) 623, f. 8; Philcox in Dassan., Revis. Handb. Fl. Ceylon 11 (1997) 111. — Lectotype (designated here): *Thwaites CP 3570* (lecto K, barcode K000246867; isolecto A*, barcode A00048874, CAL, barcodes CAL0000023670, CAL0000023671, FR*, barcode FR0036074, G-DC*, barcodes G00319812, G00319788, GH*, barcode GH00048873, K, barcodes K000246866, K000246868, K000246869, NY*, barcode NY00273343, P, barcodes P00717116, P00717117, P00717118), Sri Lanka, Central Province, Madamahanewera.

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

Distribution — India (Travancore) and Sri Lanka.

Habitat & Ecology — Flowering: February to June.

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

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

Trigonostemon pachyphyllus Airy Shaw, Kew Bull. 25 (1971) 546; Kew Bull. 26 (1972a) 347; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 27; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 581. — Type: *Kerr 19429* (holo K, barcode K000959302), Thailand, Trang, Khao Soi Dao.

Shrubs, c. 1.5 m tall; flowering branches 3.2–4 mm diam, glabrescent. *Outer bark* c. 0.1 mm thick, brown; inner bark 0.1–0.2 mm thick, reddish brown; wood yellow. *Stipules* subulate, 0.6–0.8 mm long, caducous, pubescent. *Leaves*: petiole wrinkled, flat or slightly grooved above, 0.3–1 cm long, 2–2.2 mm diam, pubescent to glabrous; blade oblong, 12–19 by 2.1–3.9 cm, coriaceous, base acute, adaxial glands not seen, margin entire, occasionally with very sparse glandular teeth, apex acuminate, upper surface glabrous, dull green or puplish brown when dry, lower surface sparsely pubescent, yellow when dry; venation pinnate, midrib flat above and elevated beneath, often pubescent beneath, secondary veins 12–15 pairs, curved, bifurcate and connected along margin, tertiary veins reticulate. *Inflorescences* seemingly unisexual; staminate ones axillary, thyrses, axis 1–1.4 cm long, 0.8–1.1 mm diam, pubescent, bracts triangular, 0.15–1.3 by 0.2–0.6 mm, pubescent; pistillate ones terminal or axillary, racemes, axis up to 1.5 cm long, 0.6–1.1 mm diam, pubescent, bracts lanceolate, 0.6–2.5 by 0.3–0.8 mm, pubescent outside. *Staminate flowers* at least 3.5 mm diam; pedicel c. 1.2 mm long, c. 0.35 mm diam, pubescent; sepals elliptic, 1–1.7 by 0.3–0.8 mm, base connate, margin entire, apex acute, pubescent or hirsute outside; petals obovate, 3.4–4.5 by 1.4–2. 5 mm, dark red-purple, glabrous; disc lobes rectangular, 0.35–0.5 by 0.35–0.45 mm, apex truncate to slightly rounded; stamens 5, anthers ellipsoid, 0.8–1 mm long, apically divaricate. *Pistillate flowers* (fruiting) 6–10.5 mm diam; pedicel thickening towards apex, 3.6–4.5 mm long, apically 1.5–2 mm diam, pubescent; sepals triangular to lanceolate, 8.5–10 by 3.5–4.6 mm, outer surface pubescent, sometimes marbled, mixed patches in dark red and yellow, inner surface glabrous, dark purplish red when dry, base connate, margin distantly serrate, teeth glandular, apex acuminate, ending in a gland; petals fallen, not seen; disc lobes semi-orbicular, 0.7–0.9 by 0.45–0.6 mm, apex rounded; ovary c. 1.5 mm diam, densely pubescent; style c. 0.2 mm long; stigmas apically deeply bifid, free arms 0.5–0.6 mm long. *Fruits* c. 1 cm diam, green; sepals persistent, green. *Seeds* not seen.

Distribution — Thailand (Trang and Phatthalung, endemic).

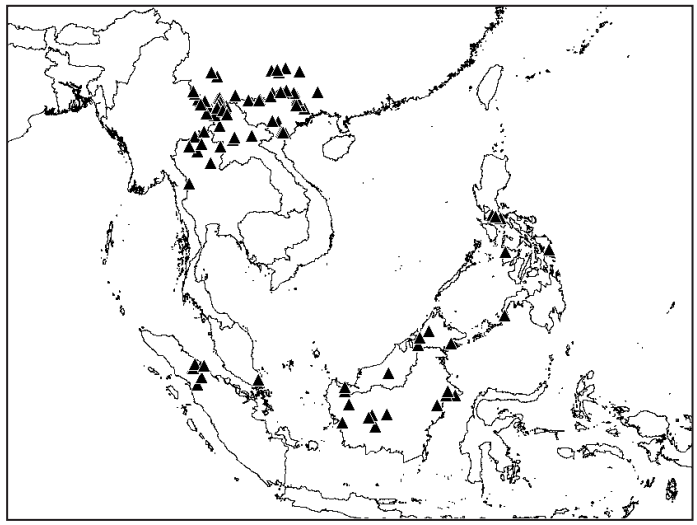
Habitat & Ecology — Evergreen forests, understorey, near streams. Flowering: March to April; fruiting: April.

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

23. ***Trigonostemon philippinensis*** Stapf — sect. ***Tylosepalum*** — Map 31

Trigonostemon philippinensis Stapf, Leafl. Philipp. Bot. 1 (1907) 206 (‘*philippinense*’); Pax & K.Hoffm. in Engl., Pflanzenfam. IV.147.iii (1911) 91; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 452; Airy Shaw, Kew Bull. 36 (1981) 355; Alphab. Enum. Euphorb. Philipp. Isl. (1983b) 47; R.I.Milne, Kew Bull. 50 (1995a) 27, in key, 29, in key. — Lectotype (designated here): *Elmer 8326* (lecto K, barcode K000959370; isolecto BO, sheet no. BO1298668, G, barcode G00435099, L, barcode L.2260355), Philippines, Luzon, Laguna prov., Los Baños, Mt. Maquiling [= Mt. Makiling].

Trigonostemon thyrsoideus Stapf, Bull. Misc. Inform. Kew (1909) 264 (‘*thyrsoideum*’); Airy Shaw, Kew Bull. 26 (1972a) 348; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 166; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 29; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 584, pl. 32: 1; P.T.Li & M.G.Gilbert in C.Y.Wu, P.H.Raven & D.Y.Hong, Fl. China 11 (2008) 274. — Type: *Henry 11947* (A*, barcodes A00048871, A00048872, K, barcode K000959335, NY*, barcode NY00273339), China, Yunnan, Simao (Szemao).



Map 31 Distribution of *Trigonostemon philippinensis* Stapf.

Trigonostemon laoticus Gagnep., Bull. Soc. Bot. France 69 (1922) 751. — *Prosartema laotica* (Gagnep.) Gagnep., Bull. Soc. Bot. France 71 (1925a) 876; in Lecomte, Fl. Indo-Chine 5 (1925b) 306, *syn. nov.* — Type: *Thorel s.n.* (P, barcodes P00717113, P00717114, P00717115), Laos, Luang-prabang.

Prosartema stellaris Gagnep., Bull. Soc. Bot. France 71 (1924b) 875; in Lecomte, Fl. Indo-Chine 5 (1925b) 304. — *Trigonostemon stellaris* (Gagnep.) Airy Shaw, Kew Bull. 32 (1978) 415, *syn. nov.* — Syntypes: *Balansa 3322* (P, barcodes P00717163, P00717164, P00717165); *Balansa 3323* (P, barcode P00717162); *Balansa 3324* (P, barcodes P00717160, P00717161), Vietnam, Tokin, Langkok (Mt. Bavi) valley.

Trigonostemon nigrifolius N.P.Balakr. & Chakrab., J. Econ. Taxon. Bot. 5 (1984b) 173; Candollea 46 (1991) 625, f. 9, *syn. nov.* — Type: *Po Khaut 12434* (holo DD*), Myanmar, Maymyo Dist., Gokteik viaduct.

Description see Yu & van Welzen 2018.

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

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

24. ***Trigonostemon quocensis*** Gagnep. — sect. ***Tylosepalum*** — Map 25

Trigonostemon quocensis Gagnep., Bull. Soc. Bot. France 69 (1922) 753; in Lecomte, Fl. Indo-Chine 5 (1925b) 316; Airy Shaw, Kew Bull. 26 (1972a) 348; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 27; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 582. — Lectotype (designated here): *Pierre s.n.* (lecto P, barcode P00717135; isolecto K barcode K000959314, P, barcodes P00717136, P00717138), Vietnam, Phu Quoc. — Other syntypes: *Godefroy 739* (P, barcodes P00717131, P00717132), Vietnam, Ha-tien; *Godefroy 740* (P, barcode P00717130), Vietnam, Ha-tien; *Harmand 632* (P, barcodes P00717128, P00717129), Vietnam, Nui Cam; *Pierre 6232* (G*, barcode G00435097, P, barcodes

P00717133, P00717134, P00717137, MPU*, barcodes MPU015001, MPU015002, NY*, barcode NY00273345), Vietnam, Chaudoc, Mt. Pell.

Trigonostemon birmanicus Chakrab. & N.P.Balakr., J. Econ. Taxon. Bot. 5 (1984a) 175; N.P.Balakr. & Chakrab., Candollea 46 (1991) 613, f. 2, *syn. nov.* — Type: *Chin* [collector's name uncertain] *5849* (holo CAL, barcode CAL0000023654), Myanmar, Upper Chindwin, Numpakom drainage.

Shrubs or small trees, 0.5–5 m tall, dhb 6–8 cm; flowering branches 1–3.8 mm diam, pubescent when young, glabrous in old parts. *Indumentum* of simple hairs; translucent (oil?) dots sometimes present in green parts. *Outer bark* 0.1–0.2 mm thick, dark brown; inner bark 0.1–0.2 mm thick, reddish brown, solidified sap reddish black; wood yellow. *Stipules* subulate, 0.2–0.7 mm long, caducous, sometimes pubescent at base. *Leaves*: petiole terete, (0.6–)1–6.1 cm long, 0.8–2 mm diam, glabrous or pubescent, sometimes thickened at apex and base; blade ovate to elliptic, 8–24 by 3.6–10 cm, chartaceous, base truncate, rounded, acute or sometimes cordate, 2 adaxial glands present, sometimes pubescent, margin distantly serrate, apex acuminate to caudate, both surfaces pubescent when young, glabrous when mature; venation triplinerved (basal secondary veins often as thick as other secondary veins), midrib and sometimes secondary veins flat or slightly raised above and distinctively elevated and pubescent beneath, other secondary veins 6–9 pairs, bow-shaped and connected along margin, tertiary veins scalariform, veinlets reticulate. *Inflorescences* bisexual, terminal or axillary, large panicles, pistillate flowers open before staminate ones; main axis terete, up to 44 cm long, 0.6–1.5 mm diam, pubescent; bracts linear to lanceolate, 1–12 by 0.15–1(–2.1) mm, often pubescent. *Staminate flowers* 4.4–5.5 mm diam, buds usually globose; pedicel 3.5–7.5 mm long, 0.15–0.3 mm diam, glabrous; sepals ovate to elliptic, 1.4–2.5 by 0.8–2.2 mm, base connate, margin entire, apex acute to rounded, pubescent outside; petals obovate to flabellate, 2.1–3.9 by 1.7–2.5 mm, contort, yellow, lower part sometimes claw-like, apex rounded, glabrous; disc annular, fleshy, margin entire, 0.4 (inner margin)–0.8 mm (outer margin) diam; stamens 3, androphore 0.3–0.6 mm long, 0.2–0.3 mm diam, filament free part 0.4–0.5 mm long, anthers free, globose to ellipsoid, 0.4–0.5 mm long. *Pistillate flowers* 6–7 mm diam, buds somewhat conical; pedicel thickened toward apex, 2–5.5 mm long, apically 0.5–0.9 mm diam when flowering, elongating to 4–9 mm long, apically 0.6–1 mm diam when fruiting, pubescent; sepals lanceolate to elliptic, 1.5–4.5 by 0.7–1.6 mm, base connate, margin entire, apex acute to acuminate; petals and disc as staminate flowers; ovary 1–1.2 mm diam, densely pubescent, style indistinct, stigmas 0.4–1 mm long, slightly thickened and sometimes slightly bifid at apex. *Fruits* 1–1.1 cm diam, hirsute; sepals persistent, but not accrescent; wall 0.3–0.4(–0.5) mm thick, exocarp not detaching; columella 4.5–6.5 mm long. *Seeds* 6–7 mm diam, marbled; hilum orbicular or rhombic, 1.2–1.7 by 1.1–1.5 mm.

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

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

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

25. ***Trigonostemon reidioides*** (Kurz) Craib — sect. ***Spinipollen*** — Map 32

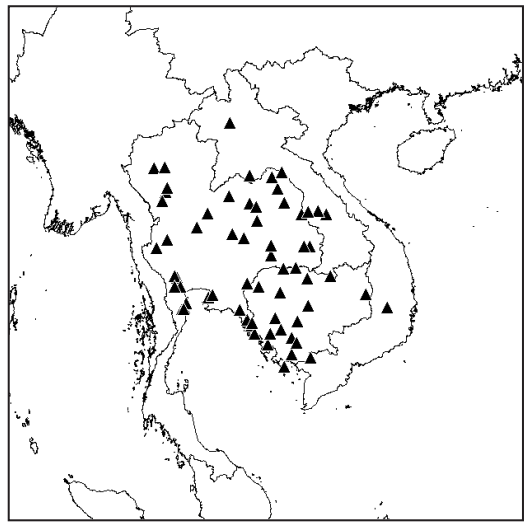
Trigonostemon reidioides (Kurz) Craib, Bull. Misc. Inform., Kew (1911) 464; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.vi (1912c) 128; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1925b) 316; Airy Shaw, Kew Bull. 26 (1972a) 348; Chantar., Thai Forest Bull. (Bot.) 33 (2005) 28; in Welzen

& Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 582. — *Baliospermum reidioides* Kurz, Flora 58 (1875) 32; Forest Fl. Burma 2 (1877b) 411; Hook.f., Fl. Brit. India 5 (1887) 461; F.N.Williams, Bull. Herb. Boiss. Ser. 2, 5 (1905) 32; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iv (1912a) 29. — Lectotype (designated here): *Teijsmann HB 5981* (lecto K, barcode K000959313; isolecto U, barcode U.1260354), Thailand, Kanburi [= Kanchanaburi]. — Other syntype: *Teijsmann s.n*. (CAL, barcode CAL0000023659), Thailand.

Trigonostemon hybridus Gagnep., Bull. Soc. Bot. France 69 (1922) 750; in Lecomte, Fl. Indo-Chine 5 (1925b) 318, *syn. nov*. — Lectotype (designated here): *Pierre 6282* (lecto P, barcode P00717109), Vietnam, Phu-Quoc (other duplicates are syntypes of the next name).

Trigonostemon rubescens Gagnep., Bull. Soc. Bot. France 69 (1922) 754; in Lecomte, Fl. Indo-Chine 5 (1925b) 317, *syn. nov*. — Lectotype (designated here): *Thorel 2290* (lecto P, barcode P00717140; isolecto NY*, barcode NY00273346, P, barcodes P00717141, P00717142, US*, barcode US00096544), Laos, Kong et île de Khon. — Other syntypes: *Pierre 6281* (P, barcodes P00717139, P00648668, P00648669, P00648670), Cambodia, Kompong Spen, Mont Ramcon; *Pierre 6282* (K, barcode K000959312, P, barcodes P00717143, P00717144, P00717145), Vietnam, Phu-Quoc.

Shrubs, 0.5–1.5 m tall; flowering branches 1.2–3.2 mm diam, slightly to densely pubescent. *Indumentum* of simple and stellately bundled hairs. *Outer bark* c. 0.1 mm thick, greyish to dark brown; inner bark 0.1–0.2 mm thick, dark reddish, sap clear, watery, black or dark red in dry material; wood yellow or brown. *Stipules* acicular to subulate, 0.6–2.3 mm long, caducous, pubescent at base. *Leaves*: petiole terete, slightly grooved above, 0.5–2.5 cm long, 0.6–1.9 mm diam, densely pubescent to glabrescent; blade oblong to elliptic, rarely obovate or (ob) lanceolate, 3.5–15 by 0.5–6.3 cm, chartaceous to coriaceous, base acute to rounded, adaxial glands 2, falcate, blackish, margin entire, apex acute to acuminate, upper surface dull dark green, lower surface dull light green, both surfaces densely to slightly pubescent, when slightly pubescent then often only simple hairs present; venation triplinerved, pubescent on both sides, midrib and basal secondary veins flat above and elevated below, other secondary veins 2–8 pairs, bow-shaped and connected along margin, tertiary veins and veinlets reticulate. *Inflorescences* bisexual, axillary or terminal large panicles; main axis terete, 3–29 cm long, 0.4–



Map 32 Distribution of *Trigonostemon reidioides* (Kurz) Craib.

1.2 mm diam, dull red, often pubescent, rarely glabrescent; bracts lanceolate to linear, 0.5–17 by 0.1–1.9 mm, pubescent. *Staminate flowers* 4.1–6.6 mm diam; pedicel 2.5–7 mm long, 0.15–0.5 mm diam, pale light green to dull reddish, pubescent to glabrescent; sepals elliptic, 1–2.6 by 0.5–1.6 mm, pale light green to dull light yellow or reddish, base connate, margin entire, sometimes ciliate, apex acute to rounded, pubescent to glabrescent outside; petals obovate to spathulate, 3.3–6.4 by 1.6–4.2 mm, white, dark red, deep maroon or dark purple, lower part sometimes claw-like, apex rounded, glabrous; disc annular, somewhat plicate, light orange, glabrous, margin undulate, 0.3–0.45 mm wide; stamens 3, androphore 0.35–0.7 mm long, 0.2–0.5 mm diam, cream, anthers ellipsoid, 0.5–0.8 mm long, cream. *Pistillate flowers* 5.3–8.9(–13) mm diam; pedicel slightly thickened toward apex, 8–20 mm long, apically 0.4–1 mm diam when flowering, elongating in fruit to (0.8–)1.6–3.4 cm long, apically 0.7–1.5 mm diam, pubescent, glabrescent; sepals elliptic to oblong, 3–6 by 1.1–2.2 mm, base connate, margin entire, sometimes ciliate, apex acute to acuminate, pubescent outside; petals as staminate flowers but larger, 5.9–9 by 2.6–6 mm; disc as staminate flowers; ovary 1.3–1.6 mm diam, pubescent, light yellow or green, style absent, stigmas thickened towards apex, 0.7–0.8 mm long, apically 0.5–0.6 mm wide, white, pale light yellow or cream, with furrowed above, apically not bifid. *Fruits* 1–1.3 cm diam, green, pubescent; sepals persistent but not accrescent; wall 0.4–0.6 mm thick, exocarp partly detaching; columella 4.2–5.8 mm long. *Seeds* 4.6–6.3 mm diam, often marbled; hilum oblong to elliptic to triangular, 0.7–1.8 by 0.5–1 mm.

Distribution — Thailand, Laos, Cambodia, Vietnam.

Habitat & Ecology — Often in open areas in dry dipterocarp forests, or in seasonal deciduous pine or *Melaleuca* forests, occasionally in waste lands or swampy forests. Often growing in sandy or rocky soil, sometimes along roads or rivers. Elevation: 20–300 m. Flowering: all year round; fruiting: January to June, August and October.

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

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

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

Trigonostemon semperflorens (Roxb.) Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1110; Hook.f., Fl. Brit. India 5 (1887) 397; Brandis, Indian Trees (1906) 580; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 90; Kanjilal & al., Fl. Assam 4 (1940) 196; N.P.Balakr., Fl. Jowai 2 (1983) 427; N.P.Balakr. & Chakrab., Candollea 46 (1991) 628, f. 10. — *Clutia semperflorens* Roxb., Fl. Ind. (Roxburgh) 3 (1832) 730; Voigt, Hort. Suburb. Calcutt. (1845) 155. — *Silvaea hookeriana* Baill., Étude Euphorb. (1858) 342, nom. superfl. — *Trigonostemon hookerianus* (Baill.) Müll. Arg. in A.DC., Prodr. 15, 2 (1866) 1109, nom. superfl. — Lectotype (designated by Yu et al. 2019b): Roxburgh's Flora Indica drawing, no. 2401 (CAL).

Small trees, 1–2.5 m tall; flowering branches 2.2–4.4 mm diam, pubescent when young, glabrous in older parts. *Outer bark* 0.1–0.2 mm thick, pale brown; inner bark 0.1–0.2 mm thick, dark red; wood pale yellow, pith hollow. *Stipules* subulate, 0.7–2.5 mm long, caducous. *Leaves*: petiole terete but often furrowed above, 2.5–9 mm long, 1.5–2.7 mm diam, pubescent; blade oblanceolate, cuneately narrowed in the lower part, 8–32 by 2.8–5.9 cm, chartaceous, base abruptly rounded to truncate, adaxial glands not seen, margin distantly serrate, teeth falcate when young, glandular or nipple-like when mature, apex acuminate to caudate, both surfaces glabrous; venation pinnate, midrib elevated on both sides, slightly pubescent on both sides, secondary veins 12–18 pairs, tertiary veins reticulate. *Inflorescences* unisexual or bisexual, rami- and cauliflorous, in short cymes or thyrses, or a single to a few flowers on short brachyblasts; peduncle 1.5–11 mm long, 0.5–0.9 mm diam, pubescent; bracts oblong to lanceolate, 0.3–5.6 by 0.2–1 mm, pubescent. *Staminate flowers* 3.8–4.9 mm diam; pedicel 2.2–2.5 mm long, 0.2–0.3 mm thick, glabrous; sepals elliptic, often unequal, 1–1.8 by 0.8–1.3 mm, base connate, margin entire, sometimes slightly ciliate, apex acute to rounded, pubescent outside; petals obovate to elliptic, 1.8–2.8 by 1.1–1.8 mm, base claw-like, apex rounded, glabrous, purple; disc lobes trapezoid, 0.2–0.3 by 0.2–0.25 mm, recurved at apex, glabrous; stamens 3, androphore 0.5–0.6 mm long, c. 0.1 mm diam; anthers free, divaricate at apex, thecae 0.4–0.5 mm long, connective with numerous droplets with secretion. *Pistillate flowers* (fruiting) 4.2–5.3 mm diam; pedicel c. 1 mm long, c. 0.5 mm diam when flowering, elongating in fruit to 2.5–4 mm long, 1.2–1.4 mm diam, glabrous to slightly pubescent; sepals elliptic to lanceolate, 1.1–2.5 by 0.65–1.2 mm when flowering, slightly accrescent to c. 5 by 2.1 mm when fruiting, base connate, margin entire or with 2 apical teeth, apex acute, pubescent outside; petals elliptic, c. 3.2 by 1.7 mm, base claw-like, apex rounded; disc not seen; ovary 1.5–1.8 mm diam, densely pubescent; stigmas 0.4–0.5 mm long, apically deeply bifid. *Fruits*: sepals persistent; columella 4–6 mm log. S*eeds* not seen.

Distribution — NE India and Bangladesh.

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

Note — see note under *T. flavidus*.

27. ***Trigonostemon tuberculatus*** F.Du & Ju He — sect. ***Tylosepalum*** — Map 22

Trigonostemon tuberculatus F.Du & Ju He, Kew Bull. 65 (2010) 111, f. 1, 2. — Type: *Du*, *He* & *Zhang 200401* (holo SWFC, not seen), China, Yunnan, Yuanjiang.

Shrubs, up to 2 m tall; flowering branches 2.3–2.5 mm diam, densely pubescent. *Bark* 0.1–0.2 mm thick, pale brown; wood yellow to brown. *Stipules* subulate, 0.5–0.7 mm long, caducous, densely pubescent at base, often buried in hairs. *Leaves*: petiole terete, 1.4–3.3 cm long, 0.8–1 mm diam, densely pubescent; blade ovate, 4.4–6.9 by 1.6–4.7 cm, coriaceous, base acute to truncate, 2 adaxial glands present, margin distantly serrate, teeth glandular, apex acute, both surfaces densely pubescent; venation often palmate, densely pubescent on both sides; midrib and basal secondary veins slightly elevated on both surfaces, other secondary veins 5–7 pairs, bifurcate and connected along margin, tertiary veins scalariform, obscure, veinlets reticulate, obscure. *Inflorescences* seemingly unisexual, axillary or terminal panicles; main axis terete, 2.7–5 cm long, 0.5–1 mm diam, densely pubescent; bracts lanceolate, 0.8–1.8 by 0.5–0.8 mm, densely pubescent. *Staminate flowers* 4.1–6.1 mm diam; pedicel 1.6–2.7 mm long, 0.3–0.5 mm diam, densely pubescent; sepals elliptic, 1.5–3 by 0.9–1.5 mm, base connate, margin entire, apex acute, pubescent outside; petals spathulate, 3–3.8 by 1.4–2 mm, apex rounded, yellow, glabrous; disc annular, c. 0.4 mm wide, pubescent; stamens 3, androphore 0.9–1 mm long, 0.15–0.2 mm diam, anthers ellipsoid, 0.6–0.7 mm long. *Pistillate flowers* (Du et al. 2010): sepals elliptic, c. 3 mm long, with buff vesicles, densely tomentose outside; petals narrowly

elliptic, c. 4 mm long, glabrous, with or without 1 or 2 dichotomous glands; disc unknown; ovary tuberculate, densely long tomentose, stigmas bifid at apex. *Fruits* (Du et al. 2010) oblate, c. 3 cm diam, green when young, warts 1–2 mm diam. *Seeds* (Du et al. 2010) flat, elliptic, 0.9–1 cm long, c. 0.6 mm diam; aril c. 1 mm thick, spongy, green.

Distribution — China (Yuanjiang, Yunnan; endemic).

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

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

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

28. ***Trigonostemon verticillatus*** (Jack) Pax var. ***verticillatus —*** sect. ***Trigonostemon*** — Map 33

Trigonostemon verticillatus (Jack) Pax in Engl., Planzenfam. IV.147.iii (1911) 87; Jabl., Brittonia 15 (1963) 164; Airy Shaw, Kew Bull. 26 (1972a) 349; Whitmore, Tree Fl. Malaya 2 (1973) 136; Chantar.,Thai Forest Bull. (Bot.) 33 (2005) 30; in Welzen & Chayam. in Santisuk & K.Larsen, Fl. Thailand 8, 2 (2007) 585, pl. 31: 2; R.Y.Yu & Welzen, Blumea 62 (2018) 213. — *Enchidium verticillatum* Jack, Malayan Misc. 2, 7 (1822) 90; Comp. Bot. Mag. 1 (1835) 257, excl. synon. Rumphius; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 1256; Merr., J. Arnold Arbor. 33 (1952) 224. — Neotype (designated by Yu & van Welzen 2018): *Maingay 1403* (neo L, barcode L.2258683; isoneo: BM, CAL, barcode CAL0000031928, K), Malay Peninsula, Malacca.

Telogyne indica Baill., Étude Euphorb. (1858) 328, pl. 11, f. 13. — *Trigonostemon indicus* (Baill.) Müll.Arg., Linnaea 34 (1865) 214; in A.DC., Prodr. 15, 2 (1866) 1107; Hook.f., Fl. Brit. India 5 (1887) 398; Ridl., Fl. Malay Penins. 3 (1924) 264; Jabl., Brittonia 15 (1963) 152. — Lectotype (designated by Yu & van Welzen 2018): *Wallich 7997* (lecto G*, barcode G00435096; isolecto G*, no barcode; G-DC*, barcode G00319770, on 2 sheets, K, barcodes K000959330, K000959331, K000959332, K000959333, P, barcode P00717110), Malaysia, Penang.

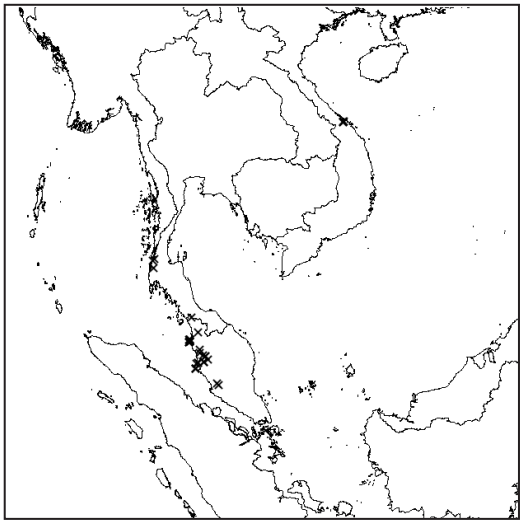
Description and taxonomic notes see Yu & van Welzen 2018.

Distribution — Thailand, Malay Peninsula.

29. ***Trigonostemon villosus*** Hook.f. var. ***nicobaricus*** (Chakrab.) N.P.Balakr. & Chakrab. — sect. ***Trigonostemon*** — Map 27

Trigonostemon villosus Hook.f. var. *nicobaricus* (Chakrab.) N.P.Balakr. & Chakrab., Candollea 46 (1991) 629, f. 11. — *Trigonostemon nicobaricus* Chakrab., J. Econ. Taxon. Bot. 5 (1984) 203. — Type: *Dwivedi 8521A* (holo CAL, barcode CAL0000023667), *Dwivedi 8521B* (iso PBL, not seen), *Dwivedi 8521C* (iso PBL, not seen), *Dwivedi 8521D* (iso PBL, not seen), *Dwivedi 8521E* (iso PBL, not seen), India, Great Nicobar Island, 9km on East-West road.

Small trees, 5–7 m tall; flowering branches 2.8–3.8 mm diam, pubescent when young. *Outer bark* c. 0.1 mm thick, flaky, pale brownish; inner bark c. 0.1 mm thick, dark reddish; wood pale yellow. *Stipules* subulate, 0.8–1 mm long, caducous. *Leaves*: petiole terete but grooved above, 0.3–1 cm long, c. 2.3 mm diam, pubescent; blade oblanceolate, 6.5–23.8 by 2.1–5.6 cm, chartaceous, base abruptly narrowed, rounded to obtuse, 2 adaxial glands present, margin distantly serrate, apex acuminate to caudate, upper surface glabrescent, slightly pubescent



Map 33 Distribution of *Trigonostemon verticillatus* (Jack) Pax. var. *verticillatus*.

beneath; venation pinnate; midrib slightly raised above and elevated beneath, secondary veins 13–18 pairs, slightly curved and connected along margin, tertiary veins reticulate. *Inflorescences* unisexual, terminal or axillary, staminate ones racemose thryses, pistillate ones racemes; axis up to 4.8–11.7 cm long, 0.4–0.6 mm diam, slightly pubescent; bracts lanceolate to elliptic, 1.5–7 by 0.4–0.7 mm, pubescent outside. *Staminate flowers* (Chakrabarty 1984): pedicel 2–5 mm long, apically 0.4–0.7 mm diam, basally 0.1–0.3 mm diam, puberulous; sepals oblong to triangular, 1–1.5 by 0.7–1.2 mm, margin ciliate, puberulous outside; petals spathulate to obovate, c. 2.5 by 1.2–1.5 mm, blackish-crimson, pilose to glabrous; disc glands c. 0.5 mm long; stamens 3, androphore 1–1.3 mm long, anthers ellipsoid to orbicular, 0.6–0.7 mm long. *Pistillate flowers* (Chakrabarty 1984): pedicel 3.5–4 mm long, apically c. 1 mm diam, basally c. 0.5 mm diam, tomentose; sepals ovate to lanceolate, 4–6 by 1.5–2 mm, margin denticulate to entire, apex acuminate, puberulose outside, without gland or appendage; petals oblong to elliptic, c. 2 by 1–1.2 mm, blackish-crimson, sparsely pilose outside; disc glands c. 0.5 mm long; ovary c. 1 mm diam, densely puberulose, stigmas c. 0.8 mm long, erect and apically bifid. *Fruits* and *seeds* not seen.

Distribution — India (Great Nicobar island, endemic).

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

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

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

30. ***Trigonostemon viridissimus*** (Kurz) Airy Shaw — sect. ***Tylosepalum*** — Map 34

Trigonostemon viridissimus (Kurz) Airy Shaw, Kew Bull. 25 (1971) 545; Whitmore, Tree Fl. Malaya 2 (1973) 135; Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 205; Kew Bull. 36 (1981)

358; Kew Bull. 37 (1982a) 36; Alphab. Enum. Euphorb. Philipp. Isl. (1983) 48; N.P.Balakr. & Chakrab., Candollea 46 (1991) 631, f. 12; R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 29, in key; R.Y.Yu & Welzen, Blumea 62 (2018) 221. — *Sabia viridissima* Kurz, J. Asiat. Soc. Bengal part 2, Nat. Hist., 41 (1872) 304; Hook.f., Fl. Brit. India 2 (1876) 3; Kurz, Forest Fl. Burma 1 (1877a) 301. — *Blachia viridissima* (Kurz) King, J. Asiat. Soc. Bengal 65 (1896) 455, in obs. — *Kurziodendron viridissimum* (Kurz) N.P.Balakr., Bull. Bot. Surv. India 8 (1966) 68, pl. 1, f. 1–7. — Lectotype (designated here): *Kurz s.n*. (lecto K, barcode K000246872; isolecto K, barcode K000246871), India, Andamans.

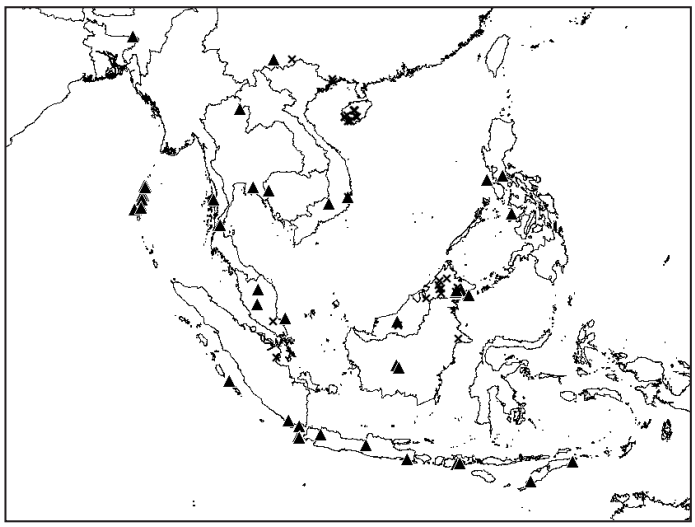
Neotrigonostemon diversifolius Pax & K.Hoffm., Notizbl. Bot. Gart. Berlin-Dahlem 10 (1928) 385; in Engl. & Harms, Nat. Pflanzenfam. ed. 2, 19c (1931) 169. — Type: *Parker 2593* (K), Myanmar, Mergui, Ngawun Reserve.

Trigonostemon chatterjii Deb & G.K.Deka, Indian Forester 91 (1965) 577; N.P.Balakr., Fl. Jowai 2 (1983) 427. — *Trigonostemon viridissimus* (Kurz) Airy Shaw var. *chatterjii* (Deb & G.K.Deka) N.P.Balakr. & Chakrab., J. Econ. Taxon. Bot. 5 (1984c) 967; Candollea 46 (1991) 635; Talukdar et al., Science Research Reporter 5 (2015) 10, *syn. nov*. — Type: *Deka 19A* (holo CAL), *Deka 19B* (iso ASSAM*), *Deka 19C* (iso ASSAM*), *Deka 19D* (iso ASSAM*), *Deka 19E* (iso ASSAM*), India, Meghalaya, Jowai dist., Dawki.

Trigonostemon viridissimus (Kurz) Airy Shaw var. *confertifolius* N.P.Balakr. & N.G.Nair, Bull. Bot. Surv. India 24 (1982) 36; N.P.Balakr. & Chakrab., Candollea 46 (1991) 635, *syn. nov*. — Type: *Balakrishnan & Nair 4773A* (holo CAL, not found), *Balakrishnan & Nair 4773B* (iso L, not found), *Balakrishnan & Nair 4773C* (iso PBL, not seen), *Balakrishnan & Nair 4773D* (iso PBL, not seen), *Balakrishnan & Nair 4773E* (iso PBL, not seen), India, North Andamans, Saddle Peak.

Trigonostemon huangmosu Y.T.Chang, Guihaia 3 (1983) 174; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 167. — Type: *Lüchun Exped. 1961* (KUN, barcodes KUN1294366, KUN1294367), China, Yunnan, Gejiu.

Shrubs or small trees, 1–10 m tall, stem to 10 cm diam; flowering branches 1.5–3.2(–4.6) mm diam, pubescent when young, glabrescent. *Indumentum* of simple hairs; translucent (oil?) dots often present in green parts. *Bark* 0.1–0.3 mm thick, grey or pale to reddish brown or grey;



Map 34 Distribution of *Trigonostemon viridissimus* (Kurz) Airy Shaw var. *viridissimus* (▲) and *T. viridissimus* var. *elegantissimus* (Airy Shaw) Airy Shaw (×).

wood pale yellowish, pith sometimes hollow. *Stipules* subulate to nipple-like, 0.4–1.5 mm long, caducous, often pubescent at base. *Leaves*: petiole terete but grooved above, 0.5–3.5(–5.5) cm long, 0.7–1.8 mm diam, wrinkled, pubescent when young; blade ovate to elliptic to oblong, sometimes (ob)ovate, (4.5–)8–24 by (1.5–)2.5–9 cm, membranous to chartaceous, base acute or obtuse, often with 1 or 2 pairs of adaxial glands, margin entire or slightly distantly serrate, apex acuminate to caudate, upper surface glabrescent to glabrous, dark green, lower surface often sparsely pubescent, paler and dull green; venation triplinerved, midrib slightly raised above and elevated beneath, often pubescent, especially near base, secondary veins 5–10 pairs, bow-shaped and connected along margin, tertiary veins scalariform, veinlets reticulate. *Inflorescences* bisexual, terminal or axillary, loose panicles; main axis terete, to 30 cm long, 0.4–2 mm diam, slightly pubescent; bracts lanceolate, 0.5–6 by 0.2–1 mm, pubescent. *Staminate flowers* 5–9 mm diam; buds conical; pedicel 4.5–9 mm long, 0.15–0.2 mm diam, glabrescent or slightly pubescent; sepals elliptic to orbicular to triangular, 1–1.7 by 0.6–1.2 mm, imbricate, margin somewhat undulate, apex rounded or truncate, sometimes with a short notch and an apical gland, pubescent outside; petals obovate, 3–6.5(–10) by 2.5–4.5(–7) mm, contort, membranous, with several distinct parallel veins, base cuneate or somewhat claw-like, entire, apex rounded, yellow to orange, glabrous; disc annular, margin undulate, reflexed, sometimes with 5 notches; stamens 3, androphore 0.7–1.5 mm long, free part of filaments 0.3–0.4(–0.6) mm long, anthers free, ellipsoid, 0.4–0.5 mm long. *Pistillate flowers* 5–9 mm diam; buds conical; pedicel slightly thickened toward apex, 0.3–1.4 cm long, apically 0.5–0.7 mm diam when flowering, elongating up to 1.1–2.9 cm long and 0.8–2 mm diam in fruit, glabrescent, often with oil-like dots; sepals, petals and disc as staminate flowers, petals caducous when fruiting; ovary 0.8–1.1 mm diam, glabrous, with numerous oil-like dots on surface, styles 0.2–0.7 mm long, stigmas 0.5–1.5 mm long, erect or bent, apically slightly thickened and slightly bifid or horseshoe-like. *Fruits* 1.1–1.5 cm diam, greenish, glabrous, smooth; sepals persistent but not accrescent; wall 0.4–0.5 mm thick, exocarp partly detaching; columella 5–6.3 mm long. *Seeds* 7–8 mm diam, with numerous oil-like dots on surface; hilum rhombic to oblong, 1.5 by 0.6–1.2 mm.

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

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

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

Key to the varieties

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

a. var. ***viridissimus*** — Map 34

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

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

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

b. var. ***elegantissimus*** (Airy Shaw) Airy Shaw — Map 34

Trigonostemon viridissimus (Kurz) Airy Shaw var. *elegantissimus* (Airy Shaw) Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 206; R.Y.Yu & Welzen, Blumea 62 (2018) 222. — *Trigonostemon elegantissimus* Airy Shaw, Kew Bull. 20 (1966) 48; Kew Bull. 32 (1978) 417; Whitmore, Tree Fl. Malaya 2 (1973) 135; R.I.Milne, Kew Bull. 50 (1995a) 28, in key, 29, in key, 47. — Type: *Kostermans 13695* (holo K, barcode K000959295; iso BO, sheet no. BO1722352, L, barcode L.2258606), E. Kalimantan, Sangkulirang District, Karangan River, near Batu Pondong.

Trigonostemon chinensis Merr., Philipp. J. Sci. 21 (1922b) 498; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 167; P.T.Li et al., Harvard Pap. Bot. 11 (2006) 118; P.T.Li & M.G.Gilbert in C.Y.Wu, P.H.Raven & D.Y.Hong, Fl. China 11 (2008) 274, *syn. nov*. — Type: *Tsoong 1875* (PE barcode PE01110916, PNH sheet no. 88948), China, Guangxi, Tung Sing [= Dongxing], Dongjingshan.

Trigonostemon sanguineus Gagnep., Bull. Soc. Bot. France 72 (1925a) 470. — Type: *Poilane 8201* (P, barcodes P00717146, P00717147), Vietnam, km 26 route from Nhatrang to Ninh Hoa.

Trigonostemon kwangsiensis Hand.-Mazz., Sinensia 2 (1932) 130. — Type: *Ching 7729* (A*, barcode A00048864, NY*, barcode NY00273338), China, Guangxi, Bako Schan.

Trigonostemon fungii Merr., Lingnan Sci. J. 11 (1932) 47. — *Trigonostemon chinensis* Merr. f. *fungii* (Merr.) Y.T.Chang, Acta Phytotax. Sin. 27 (1989) 149; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 169. — Type: *Tsang* & *Fung 18170* (IBSC, not found), China, Hainan. — Paratype: *Tsang* & *Fung 17606* (IBSC, barcodes IBSC0306872, IBSC0306873), China, Hainan, Hongmaoshan.

Trigonostemon leucanthus Airy Shaw var. *hainanensis* H.S.Kiu in H.S.Kiu & X.X.Chen, Guihaia 12 (1992) 211. — Type: *Liang 62132* (holo IBSC, barcode IBSC0306909, iso IBK, barcode IBK00169494), China, Hainan, Yazhou, Heiluoling, Xiaobaokang.

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

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

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

31. ***Trigonostemon xyphophylloides*** (Croizat) L.K.Dai & T.L.Wu — sect. ***Tylosepalum*** — Figure 33, Map 27

Trigonostemon xyphophylloides (Croizat) L.K.Dai & T.L.Wu in Chun et al., Acta Phytotax. Sin. 8 (1963) 277; H.S.Kiu, Fl. Reipubl. Popul. Sin. 44(2) (1996) 163; P.T.Li & M.G.Gilbert in C.Y.Wu, P.H.Raven & D.Y.Hong, Fl. China 11 (2008) 273. — *Cleidion xyphophylloides* Croizat, J. Arnold Arbor. 21 (1940) 503. — *Wang 34005* [cited as '34006' in Croizat 1940, probably a typo; marked as holotype in A by Croizat] (A*, barcode A0004596, IBK, barcode IBK00169539, IBSC, K, barcode K000959334), China, Hainan, Ya County.

Small trees, 1.5–3 m tall; flowering branches c. 3.5 mm thick, often glabrous. *Bark* 0.3–0.5 mm diam, dark brown to grey, sap reddish black when solidified; wood pale brown, pith sometimes

hollow. *Stipules* subulate, 1.9–2.4 mm long, light green, glabrous or sometimes pubescent at base. *Leaves*: petiole 0.5–3 cm long, slightly grooved above, more or less pubescent; blade oblanceolate, lower part cuneately narrowed, 22–49 by 5.4–11 cm, coriaceous, base round to truncate, adaxially 2 stipellae present, subulate to falcate to linear, 1.9–2.2 by 0.3–0.6 mm, yellow to light green, blade margin distantly serrate, teeth glandular, apex acuminate or sometimes rounded, green above, light green beneath, glabrous on both surfaces; venation pinnate, midrib slightly raised above, distinctly elevated beneath, secondary veins 13–18 pairs, slightly curved, bifurcate and connected near margin, tertiary veins reticulate. *Inflorescences* unisexual; staminate ones cauliflorous, short and condensed cymes or thyrses, bracts semi-orbicular to lanceolate, 0.3–1.8 by 0.3–1.5 mm, pubescent; pistillate ones terminal or axillary, often racemose, axis 1.5–2.4 cm long, pubescent, bracts lanceolate, 1.3–2.4 by 0.8–1 mm,

Figure 33 *Trigonostemon xyphophylloides* (Croizat) L.K.Dai & T.L.Wu, cultivated in South China Botanical Garden. a. Growing habit; b. leaf base, showing stipellae; c. branch tip, showing stipules; d. bark; e. branch, showing the ramiflorous inflorescences; f. top view of staminate flower; g. flower buds and lateral view of staminate flower; h. columella of fruit. — Photos by Ren-Yong Yu.

pubescent. *Staminate flowers* 3.1–4 mm diam; pedicel 3.1–6 mm long, 0.1–0.2 mm diam, pinkish, glabrous; sepals ovate to elliptic, 1–1.2 by 0.7–1 mm, imbricate, pinkish green, connate at base, apex often rounded, more or less pubescent outside, sometimes with an apical gland outside; petals oblong to oblanceolate, 1.5–5.3 by 0.5–1.3 mm, orange with a reddish honey mark at base, visible on both sides, apex acute, glabrous on both sides; disc glands rectangular to trapezoid, 0.25–0.35 by 0.25–0.4 mm, somewhat fleshy, apex truncate to rounded; stamens 3, androphore erect, 0.2–0.3 mm long, c. 0.3 mm diam, anthers free, divaricate, thecae 0.4–0.5 mm long, connective with an apical appendage. *Pistillate flowers* (bud) at least 2 mm in diam; pedicel c. 3 mm long, c. 0.5 mm diam, pubescent; sepals ovate to triangular, c. 1 by 0.9 mm, pubescent; petals, disc and ovary not seen. *Fruits* green, glabrous; pedicel 0.8–1 cm long, c. 2.8 mm diam; sepals persistent, slightly accrescent, c. 2 by 1.2 mm; columella 6.5–8 mm long. *Seeds* globose or ellipsoid, 0.85–0.9 by 0.7–0.85 mm, dark orange to brown when dry.

Distribution — China (Hainan, endemic?).

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

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

DOUBTFUL SPECIES

32. ***Trigonostemon praetervisus*** Airy Shaw — Map 25

Trigonostemon praetervisus Airy Shaw, Kew Bull. 37 (1982b) 121; N.P.Balakr. & Chakrab., Candollea 46 (1991) 625. — Type: *Wallich 8001* (holo K, part of the specimen, as it shares the same sheet with *Croton chlorocalyx* Müll.Arg., barcode K000246858), Bangladesh, Assam, Sylhet.

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

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

Excluded names

Trigonostemon beddomei (Benth.) N.P.Balakr., Bull. Bot. Surv. India 10 (1968) 245. = ***Tritaxis beddomei*** Benth., J. Linn. Soc., Bot. 17 (1878) 221. — *Dimorphocalyx beddomei* (Benth.) Airy Shaw, Kew Bull. 23 (1969) 124. — Type: *Beddome 37* (K, barcode K000246899), India, East-Indian Peninsula, Tinnevelly, (Yu et al. 2019b).

Trigonostemon gaudichaudii (Baill.) Müll.Arg., Linnaea 34 (1865) 213. = ***Tritaxis gaudichaudii*** Baill., Étude Euphorb. (1858) 343; Müll.Arg., Linnaea 34 (1865) 213; in A.DC., Prodr. 15, 2 (1866) 1107; Pax & K.Hoffm. in Engl., Pflanzenr. IV.147 (1911) 94; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1925b) 302; Pax & K.Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 19c (1931) 167. — Lectotype (designated by Yu et al. 2019b): *Gaudichaud 278* (lecto P, barcode P00712262; isolecto P, barcode P00712260, P, barcode P00712261), Vietnam, (Yu et al. 2019b).

Trigonostemon lawianus (Nimmo) Müll.Arg., Linnaea 34 (1865) 212; in A.DC., Prodr. 15, 2 (1866) 1105. — *Croton lawianus* Nimmo, Cat. Pl. Bombay (1839) 251; Dalzell & A.Gibson, Bombay Fl. (1861) 232. — *Dimorphocalyx lawianus* (Nimmo) Hook.f., Fl. Brit. India 5 (1887) 404. — *Dimorphocalyx glabellus* Thwaites var. *lawianus* (Nimmo) Chakrab. & N.P.Balakr., Proc. Indian Acad. Sci. (Plant Sci.) 100 (1990) 296. = ***Tritaxis glabellus*** (Thwaites) R.Y.Yu & Welzen var. ***lawianus*** (Nimmo) R.Y.Yu & Welzen in Yu, Slik & Welzen, Taxon (2019b, in press). — Type: *Gibson 19* (K, barcode K000246856), India, Bombay, Bheema Snnker, (Yu et al. 2019b).

Trigonostemon voratus Croizat in A.C.Sm., Sargentia 1 (1942c) 52. — Type: *Tabualewa 15569* (holo A*, barcode A00105962; iso BISH*, barcode BISH1003379, K, barcode K000651877, NY*, barcode NY00273356, US*, barcode US00096545), Fiji: Viti Levu, Tholo West, Mbuyombuyo, near Xamboutini. = ***Vavaea megaphylla*** C.H.Wright, Bull. Misc. Inform. Kew (1895) 102, [Meliaceae] (Smith 1952, Pennington 1969).

Trigonostemon zeylanicus (Müll.Arg.) Müll.Arg., Linnaea 34 (1865) 213. — *Tritaxis zeylanica* Müll.Arg., Flora 47 (1864a) 482. — Type: not designated, cultivated in garden. = ***Paracroton zeylanicus*** (Müll.Arg.) N.P.Balakr. & Chakrab., Kew Bull. 48 (1993) 723, (Balakrishnan & Chakrabarty 1993).

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IDENTIFICATION LIST

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

Achmad 142: 26; 280: 26; 1663: 5; 1707: cf. 3; 1773: 5 — Alston 14647: 26; 17134: 9 — Alvins 312: 30; 605: 30; 635: 30; 1136: 30; 1902: 30; 2082: 30; 2141: 26 — Ambriansyah AA 1537: 39; AA 664: 26 — Ambriansyah & Arifin AA 17: 23a; AA 220: 52d; AA 268: 23a; AA 418: cf. 23a; W 28: 23a; W 714: 23a — Ambriansyah et al. AA 1385: 23a; AA 1825: 23a — Amdjah 394: 52d — Angian 10306: cf. 23a — Ansari 1361A: 3 — Argent, Pendry & Mitchell 91165: 23a — Arifin & Ambriansyah Berau 1549: cf. 52b — Arifin et al. Berau 1456: 23a — Atkins 461: 11.

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1. **Trigonostemon adenocalyx** Gagnep.
   Trigonostemon lutescens Y.T.Chang & J.Y.Liang
2. **Trigonostemon apetalogyne** Airy Shaw
3. **Trigonostemon aurantiacus** (Kurz ex Teijsm. & Binn.) Boerl.
   Actephila aurantiaca Ridl.
   Actephilopsis malayana Ridl.
   Codiaeum aurantiacum (Kurz ex Teijsm. & Binn.) Müll.Arg.
   Tylosepalum aurantiacum Kurz ex Teijsm. & Binn.
   Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl. var. *rubriflorus* N.P.Balakr. & Chakrab.
   Trigonostemon malayanus (Ridl.) Airy Shaw
4. **Trigonostemon balgooyi** R.Y.Yu & Welzen
5. **Trigonostemon beccarii** Ridl.
   Trigonostemon longisepalus Ridl.
6. **Trigonostemon bonianus** Gagnep.
   Trigonostemon filipes Y.T.Chang & S.L.Mo
   Trigonostemon kwangsiensis Hand.-Mazz. var. *viridulis* H.S.Kiu
   Trigonostemon petelotii Merr.
7. **Trigonostemon calcicolus** (R.I.Milne) R.Y.Yu & Welzen
   Trigonostemon polyanthus Merr. var. *calcicola* R.I.Milne
8. **Trigonostemon capillipes** (Hook.f.) Airy Shaw
   Dimorphocalyx capillipes Hook.f.
9. **Trigonostemon capitellatus** Gagnep.
   Trigonostemon cochinchinensis Gagnep.
   Trigonostemon thorelii Gagnep.
   Trigonostemon verrucosus J.J.Sm.
10. **Trigonostemon cherrieri** Veillon
11. **Trigonostemon detritiferus** R.I.Milne
12. **Trigonostemon diffusus** Merr.
13. **Trigonostemon diplopetalus** Thwaites
14. **Trigonostemon dipteranthus** Airy Shaw
15. **Trigonostemon eberhardtii** Gagnep.
    Trigonostemon albiflorus Airy Shaw
    Trigonostemon harmandii Gagnep.
    Trigonostemon leucanthus Airy Shaw
    Trigonostemon leucanthus Airy Shaw var. *siamensis* H.S.Kiu
    Trigonostemon poilanei Gagnep.
    Trigonostemon wui H.S.Kiu
16. **Trigonostemon filiformis** Quisumb.
    Trigonostemon stenophyllus Quisumb.
17. **Trigonostemon flavidus** Gagnep.
    Trigonostemon heterophyllus Merr.
    Trigonostemon sunirmalii Chakrab. & N.P.Balakr.
18. **Trigonostemon fragilis** (Gagnep.) Airy Shaw
    Poilaniella fragilis Gagnep.
19. **Trigonostemon hartleyi** Airy Shaw
20. **Trigonostemon heteranthus** Wight
21. **Trigonostemon inopinatus** Airy Shaw
22. **Trigonostemon kerrii** Craib

23a. **Trigonostemon laevigatus** Müll.Arg. var. **laevigatus**
    Trigonostemon anomalus Merr.
    Trigonostemon everettii Merr.
    Trigonostemon laevigatus Müll.Arg. var. *petiolaris* Airy Shaw

23b. **Trigonostemon laevigatus** Müll.Arg. var. **croceus** (B.C.Stone) R.Y.Yu & Welzen
    Trigonostemon croceus B.C.Stone;

24. **Trigonostemon lanceolatus** (S.Moore) Pax
    Nepenthandra lanceolata S.Moore
    Trigonostemon phyllocalyx Gagnep.
25. **Trigonostemon lii** Y.T.Chang
26. **Trigonostemon longifolius** Wall. ex Baill.
    Croton longipedunculatus Elmer
    Prosartema gaudichaudii Gagnep.
    Trigonostemon elmeri Merr.
    Trigonostemon gagnepainianus Airy Shaw
    Trigonostemon honbaensis Tagane & Yahara
    Trigonostemon howii Merr. & Chun
    Trigonostemon ionthocarpus Airy Shaw
    Trigonostemon longipedunculatus (Elmer) Elmer
    Trigonostemon longipedunculatus (Elmer) Elmer var. *mollis* R.I.Milne

Trigonostemon matangensis R.I.Milne
Trigonostemon oblanceolatus C.B.Rob.
Trigonostemon ridleyi Merr. ex Jabl.

27. **Trigonostemon longipes** (Merr.) Merr.
Dimorphocalyx longipes Merr.
28. **Trigonostemon lychnos** (R.I.Milne) R.Y.Yu & Welzen
Trigonostemon polyanthus Merr. var. *lychnos* R.I.Milne
29. **Trigonostemon magnificus** R.I.Milne
30. **Trigonostemon malaccanus** Müll.Arg.
Trigonostemon laetus Baill. ex Müll.Arg.
31. **Trigonostemon merrillii** Elmer
32. **Trigonostemon montanus** R.Y.Yu & Welzen
33. **Trigonostemon murtonii** Craib
Trigonostemon pierrei Gagnep.
Trigonostemon pinnatus Gagnep.
34. **Trigonostemon nemoralis** Thwaites
35. **Trigonostemon oblongifolius** Merr.
Trigonostemon luzoniensis Merr.
36. **Trigonostemon pachyphyllus** Airy Shaw
37. **Trigonostemon palustris** R.Y.Yu & Welzen
38. **Trigonostemon pentandrus** Pax & K.Hoffm.
39. **Trigonostemon philippinensis** Stapf
Prosartema laotica (Gagnep.) Gagnep.
Prosartema stellaris Gagnep.
Trigonostemon laoticus Gagnep.
Trigonostemon nigrifolius N.P.Balakr. & Chakrab.
Trigonostemon stellaris (Gagnep.) Airy Shaw
Trigonostemon thyrsoideus Stapf
40. **Trigonostemon polyanthus** Merr.
Trigonostemon diffusus Merr. subsp. *condensus* R.I.Milne
41. **Trigonostemon quocensis** Gagnep.
Trigonostemon birmanicus Chakrab. & N.P.Balakr.
42. **Trigonostemon reidioides** (Kurz) Craib
Baliospermum reidioides Kurz
Trigonostemon hybridus Gagnep.
Trigonostemon rubescens Gagnep.
43. **Trigonostemon rufescens** Jabl.
44. **Trigonostemon sandakanensis** Jabl.
45. **Trigonostemon scopulatus** R.Y.Yu & Welzen
46. **Trigonostemon semperflorens** (Roxb.) Müll.Arg.
Clutia semperflorens Roxb.
Silvaea hookeriana Baill.
Trigonostemon hookerianus (Baill.) Müll.Arg.
47. **Trigonostemon serratus** Blume
48. **Trigonostemon sinclairii** Jabl.
49. **Trigonostemon tuberculatus** F.Du & Ju He

50a. **Trigonostemon verticillatus** (Jack) Pax var. **verticillatus**
Enchidium verticillatum Jack
Telogyne indica Baill.
Trigonostemon indicus Müll.Arg.

50b. **Trigonostemon verticillatus** (Jack) Pax var. **salicifolius** (Ridl.) Whitmore
Trigonostemon salicifolius Ridl.

51. **Trigonostemon victoriae** R.Y.Yu & Welzen

52a. **Trigonostemon villosus** Hook.f. var. **villosus**
Trigonostemon carnosulus Airy Shaw
Trigonostemon tomentellus Pax & K.Hoffm.

52b. **Trigonostemon villosus** Hook.f. var. **borneensis** (Merr.) Airy Shaw
Trigonostemon borneensis Merr.
Trigonostemon hirsutus C.B.Rob.
Trigonostemon villosus Hook.f. subsp. *caesius* R.I.Milne
Trigonostemon wenzelii Merr.

52c. **Trigonostemon villosus** Hook.f. var. **cordatus** R.Y.Yu & Welzen

52d. **Trigonostemon villosus** Hook.f. var. **merrillianus** (Airy Shaw) R.Y.Yu & Welzen
Dimorphocalyx borneensis Merr.
Trigonostemon acuminatus Merr.
Trigonostemon laxiflorus Merr.
Trigonostemon merrillianus Airy Shaw

52e. **Trigonostemon villosus** Hook.f. var. **nicobaricus** (Chakrab.) N.P.Balakr. & Chakrab.
Trigonostemon nicobaricus Chakrab.

53a. **Trigonostemon viridissimus** (Kurz) Airy Shaw var. **viridissimus**
Blachia viridissima (Kurz) King
Kurziodendron viridissimum (Kurz) N.P.Balakr.

Neotrigonostemon diversifolius Pax & K.Hoffm.
Sabia viridissima Kurz
Trigonostemon chatterjii Deb & Deka
Trigonostemon huangmosu Y.T.Chang
Trigonostemon macgregorii Merr.
Trigonostemon membranaceus Pax & K.Hoffm.
Trigonostemon ovatifolius J.J.Sm.
Trigonostemon sumatranus Pax & K.Hoffm.
Trigonostemon viridissimus (Kurz) Airy Shaw var. *chatterjii* (Deb & Deka) N.P.Balakr. & Chakrab.
Trigonostemon viridissimus (Kurz) Airy Shaw var. *confertifolius* N.P.Balakr. & N.G.Nair

53b. **Trigonostemon viridissimus** (Kurz) Airy Shaw var. **elegantissimus** (Airy Shaw) Airy Shaw
Trigonostemon chinensis Merr.
Trigonostemon chinensis Merr. f. *fungii* (Merr.) Y.T.Chang
Trigonostemon elegantissimus Airy Shaw
Trigonostemon fungii Merr.
Trigonostemon kwangsiensis Hand.-Mazz.
Trigonostemon leucanthus Airy Shaw var. *hainanensis* H.S.Kiu
Trigonostemon sanguineus Gagnep.

54. **Trigonostemon wetriifolius** Airy Shaw & Ng
55. **Trigonostemon wildeorum** R.Y.Yu & Welzen
56. **Trigonostemon xyphophylloides** (Croizat) Dai & T.L.Wu
Cleidion xyphophylloides Croizat

doubtful 57. **Trigonostemon angustifolius** Merr.
doubtful 58. **Trigonostemon praetervisus** Airy Shaw
doubtful 59. **Trigonostemon whiteanus** (Croizat) Airy Shaw
excluded 1. *Trigonostemon arboreus* Ridl. = **Omphalea malayana** Merr.
excluded 2. *Trigonostemon asahanensis* Croizat. = **Dimorphocalyx muricatus** (Hook.f.) Airy Shaw
excluded 3. *Trigonostemon beddomei* (Benth.) N.P.Balakr. = **Tritaxis beddomei** Benth.
excluded 4. *Trigonostemon bulusanensis* Elmer. = **Tritaxis malayanus** (Hook.f.) R.Y.Yu & Welzen
excluded 5. *Trigonostemon cumingii* Müll. Arg. = **Tritaxis cumingii** (Müll.Arg.) Benth.
excluded 6. *Trigonostemon forbesii* Pax. = **Wetria insignis** (Steud.) Airy Shaw
excluded 7. *Trigonostemon gaudichaudii* (Baill.) Müll.Arg. = **Tritaxis gaudichaudii** Baill.
excluded 8. *Trigonostemon lawianus* Müll. Arg. = **Tritaxis glabellus** Thwaites var. **lawianus** (Nimmo) R.Y.Yu & Welzen
excluded 9. *Trigonostemon macrophyllus* (Müll.Arg.) Müll.Arg. = **Paracroton pendulus** (Hassk.) Miq.
excluded 10. *Trigonostemon oliganthus* K.Schum. = **Cleidion papuanum** Lauterb.
excluded 11. *Trigonostemon voratus* Croizat. = **Vavaea megaphylla** C.H.Wright,
excluded 12. *Trigonostemon zeylanicus* (Müll.Arg.) Müll.Arg. = **Paracroton zeylanicus** (Müll.Arg.) N.P.Balakr. & Chakrab.

Chapter 5 Pollen morphology of *Trigonostemon* and its relatives (Euphorbiaceae)

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Abstract The pollen of *Trigonostemon* and the related genera *Dimorphocalyx*, *Ostodes*, *Tritaxis* and *Jatropha* (outgroup) has been studied with light microscopy, and scanning and transmission electron microscopy. The two major pollen types within *Trigonostemon* correlate well with macromorphological characters. Species belonging to the *Trigonostemon reidioides* type have pollen with 'croton pattern' ornamentation, a pistil with deeply divided stigmas (to at least half the length of the stigma arm) and stamens with a protruding appendage on the connective, while species of the *Trigonostemon verrucosus* type have verrucate (to almost gemmate) pollen, stigmas that are shortly cleft and stamens without an appendage on the connective. *Dimorphocalyx*, *Ostodes*, *Tritaxis* and *Jatropha* (outgroup) have similar pollen morphology, while *Trigonostemon* deviates from these genera in the absence of the 'vertically' striate ornamentation on the subunits. Therefore, when compared with an existing phylogeny of the Euphorbiaceae, the pollen characters of *Trigonostemon* appear to be derived. Moreover, because the 'croton pattern' ornamentation itself is widely shared by the 'inaperturate crotonoids', the loss of that structure in the *Trigonostemon verrucosus* type pollen is considered a further apomorphy.

Additional key words

classification
croton pattern
Dimorphocalyx
Euphorbiaceae
Ostodes
phylogeny
Tritaxis

INTRODUCTION

Trigonostemon is a genus in the Euphorbiaceae, subfamily Crotonoideae, tribe Codiaeae, subtribe *Trigonostemoniae* (Webster 2014). It contains about 60 species ranging from India to China, throughout continental southeast Asia and Malesia to northeast Australia and the west Pacific (Govaerts et al. 2000; Yu & van Welzen 2018). The circumscription of the genus was originally confined to species possessing flowers with one whorl of three (or five) connate stamens (Blume 1825). However, Müller Argoviensis (1865, 1866) adopted a wider concept of *Trigonostemon*, including the genera *Dimorphocalyx* Thwaites and *Tritaxis* Baill., which have flowers with two or three whorls of stamens. Later authors (e.g., Bentham 1878, 1880; Hooker 1887; Pax & Hoffmann 1931) retained Blume's concept of a strict view of the genus, though Webster (1994) considered *Tritaxis* as a synonym of *Trigonostemon*. The generic delimitation of *Trigonostemon* in this article is based on Yu and van Welzen (2018). *Ostodes* has flowers with 20–41 stamens, of which the inner ones are often basally united. It closely resembles *Dimorphocalyx*, making the delimitation of *Trigonostemon* even more difficult. The classification of *Trigonostemon* in previous studies (e.g., Müller Argoviensis 1866; Hooker 1887; Pax & Hoffmann 1931; Jablonski 1963) was based on a limited number of species and appeared to be unnatural in a more comprehensive revision (Yu & van Welzen 2018). A molecular phylogenetic analysis is still lacking.

Trigonostemon pollen has hardly been studied so far. The only treatment is that by Punt (1962), who briefly dealt with five *Trigonostemon* species: *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl. (mentioned by Punt as *Actephilopsis malayana* Ridl.), *Trigonostemon capitellatus* Gagnep. (as *Trigonostemon verrucosus* J.J.Sm.), *Trigonostemon chinensis* Merr. (as *Trigonostemon fungii* Merr.), *Trigonostemon longifolius* Wall. ex Baill. (as *Prosartema gaudichaudii* Gagnep. and *Trigonostemon longifolius*), and *Trigonostemon reidioides* (Kurz) Craib. He distinguished and illustrated (line drawings) two types: the *Trigonostemon reidioides* type (reticulate ornamentation) and the *Trigonostemon verrucosus* type (gemmate ornamentation). *Dimorphocalyx*, *Ostodes* and *Tritaxis* were mentioned by him as representatives of the *Croton* type ('croton pattern' ornamentation: see Material and methods section). Nowicke (1994) made an extensive exploration of the pollen morphology of the Crotonoideae, but oddly *Trigonostemon* was not included in this benchmark study. Furthermore, pollen of *Dimorphocalyx* was described by Tissot et al. (1994; *D. lawianus* (Müll.Arg.) Hook.f., LM, SEM) and Nowicke (1994; *D. luzoniensis* Merr. [= *D. malayanus* Hook.f., see van Welzen & van Oostrum 2015], SEM), pollen of *Ostodes* by Wang et al. (1995; *O. paniculata* Blume, LM), and pollen of *Tritaxis* by Erdtman (1952; *Tritaxis gaudichaudii* Baill., LM). Webster (2014) mentioned some pollen characters in the generic descriptions of *Trigonostemon*, *Dimorphocalyx* and *Ostodes*.

The aim of the present study is to explore the pollen morphology of *Trigonostemon* and the related genera *Dimorphocalyx*, *Ostodes* and *Tritaxis*, trying to gain insight in the delimitation and infrageneric classification of *Trigonostemon*.

MATERIAL AND METHODS

Pollen of 42 *Trigonostemon* species (out of about 60), three *Dimorphocalyx* species (out of about 13; van Welzen & van Oostrum 2015), one species of *Ostodes* (out of two, van Welzen & Winkel 2015) and one of *Tritaxis* (probably monotypic) was examined. Three species of *Jatropha* were added, because, based on the backbone phylogeny of the Euphorbiaceae by Wurdack et al. (2005) this genus can be considered as the local outgroup in our study; further data on *Jatropha* pollen are given by Saad & El-Ghazaly (1988) and Nowicke (1994).

The samples (see Specimens investigated) were taken from herbarium specimens present in Naturalis Biodiversity Center in Leiden (L, U) and from fresh material collected in the field.

The samples were prepared for light microscopy (LM; slides deposited at Naturalis Biodiversity Center, the Netherlands) and scanning electron microscopy (SEM), applying the 'macro-method' used by van der Ham (1990), or the 'micro-method' of Punt (1962). The latter method was applied to rare or poor herbarium material in order to avoid wasting material, and was used with the following minor modifications. During acetolysis the samples were heated on an electric hot plate instead of the metal rack used by Punt. After making LM slides, the remaining acid mix was rinsed with 96% alcohol, and subsequently with 100% alcohol until the liquid became clear. The mix needed to be rinsed at least three times to remove all acid. SEM stubs were prepared as described by van der Ham (1990). A few SEM samples were not acetolysed (see Specimens investigated section). The samples for transmission electron microscopy (TEM) were prepared as described by van der Ham (1990), applying minor modifications: fixation in 2% osmium tetroxide (OsO_4) (instead of 1%), embedding using epon/acetonitrile (1:1), and without post-staining.

LM observations and photography were done with, respectively, a Leica DM 1000 microscope and a Carl Zeiss Axio Imager M2 microscope with Axio Cam MRc5 camera, both with 1000× magnification and immersion oil. The photographs were processed using Axio Vision SE64 software. If possible (see Specimens investigated section), ten pollen grains per sample were measured. Because the pollen grains are inaperturate, polar and equatorial views could not be determined. Therefore, the dimensions of the longest axis (L) and the shortest axis (S) were noted (Table 1). For SEM, the samples were coated with platinum using a Quorum Q150tS sputter-coater, and the observations were carried out with a Jeol JSM-7600F microscope. For TEM, the observations and photography were made with a JEM-1400plus microscope. The sections (thickness: 65–85 nm) were made using an LKB ultra microtome with a Diatome Ultra 45' knife. Measurements of exine details (thickness of exine and sublayers, size of ornamentation subunits) were made based on SEM and TEM micrographs.

The terminology follows Punt et al. (2007), e.g., the 'croton pattern' is 'a characteristic type of ornamentation comprising rings of five or six (sometimes more) raised, often triangular, sexine elements arranged around a circular area, usually formed by capitate columellae (pila)'. In the present study the sexine elements are designated as 'subunits', following Nowicke (1994).

RESULTS

Trigonostemon (Figures 34, 35, 37a–d, 38, 39f, f')

Pollen grains spheroidal to ellipsoidal monads (L = 31.8–71 µm, S = 28.7–58 µm, L/S = 1–1.68), inaperturate. Exine 0.7–2 µm thick (including 0.3–1.3 µm 'high' subunits of croton pattern); endexine ± lamellate, up to 0.4 µm, continuous or absent in many places; foot layer thin (≤ 0.1 µm) or not recognisable; infratectal layer 0.2–0.6 µm, columellate; tectum reticulate or finely reticulate to rugulate. Based on ornamentation, two main types can be recognised: (1) *Trigonostemon reidioides* type (croton pattern; subunits 0.3–0.4 µm 'high', 0.1–1 µm in diameter) and (2) *Trigonostemon verrucosus* type (verrucate, sometimes almost gemmate; verrucae 0.9–1.3 µm 'high', 0.6–2.5 µm in diameter). The *T. verrucosus* type was named by Punt (1962) after *T. verrucosus* J.J.Sm., which we consider a synonym of *T. capitellatus* Gagnep. However, we maintain the original name of the pollen type. The *reidioides* type can be divided into two subtypes: (1a) *reidioides* subtype (subunits are obtuse sexine elements) and (1b) *longifolius* subtype (subunits are spines). See later and Table 2.

Table 1 *Trigonostemon* species and related taxa: pollen size. Note: L, length longest axis; S, length shortest axis.

Species	L (µm)	S (µm)	L/S
Dimorphocalyx cumingii	41 (45.5) 49	39 (42.7) 45	1.02 (1.07) 1.12
Dimorphocalyx denticulatus	57 (59.5) 65	52 (59.9) 62	1 (1.07) 1.16
Dimorphocalyx muricatus	60 (65) 68	57 (60.9) 66	1.02 (1.07) 1.16
Jatropha curcas	82 (88.5) 96	70 (80.1) 87	1.02 (1.11) 1.17
Jatropha gossypiifolia	61 (65.6) 70	58 (63.1) 67	1 (1.04) 1.06
Jatropha multifida	67 (71.5) 77	65 (69.2) 76	1.01 (1.03) 1.09
Ostodes paniculata var. *paniculata*	60 (62.7) 66	52 (56.7) 65	1 (1.11) 1.19
Trigonostemon albiflorus	56 (61) 65	45 (52.7) 63	1.02 (1.17) 1.33
Trigonostemon aurantiacus	35 (36.6) 39	31 (33.8) 37	1 (1.09) 1.16
Trigonostemon beccarii	40 (43.7) 46	25 (34.5) 40	1.1 (1.3) 1.68
Trigonostemon capillipes	38 (40.8) 45	31 (37.1) 40	1 (1.10) 1.23
Trigonostemon capitellatus	36 (39.9) 46	30 (33.6) 39	1.05 (1.19) 1.37
Trigonostemon cherrieri	50 (55) 62	41 (49) 58	1.02 (1.13) 1.27
Trigonostemon detritiferus	52 (55.6) 59	44 (48.6) 53	1.02 (1.15) 1.32
Trigonostemon dipteranthus	48 (53.8) 62	39 (46.2) 52	1.06 (1.17) 1.36
Trigonostemon flavidus	34 (41.1) 47	32 (37.7) 44	1.03 (1.09) 1.2
Trigonostemon harmandii	42 (45.3) 51	38 (41.9) 48	1.02 (1.08) 1.13
Trigonostemon heteranthus	30 (32.2) 38	27 (29.2) 32	1.03 (1.1) 1.21
Trigonostemon inopinatus	52 (59.2) 70	42 (51.5) 63	1.05 (1.15) 1.32
Trigonostemon laevigatus var. *croceus*	40 (44.6) 52	34 (39.7) 45	1.02 (1.13) 1.41
Trigonostemon laevigatus var. *laevigatus*	42 (54) 62	40 (47.2) 53	1.05 (1.14) 1.24
Trigonostemon longifolius	46 (52.7) 61	39 (48.6) 56	1 (1.09) 1.24
Trigonostemon longipes	40 (43.1) 48	32 (37.2) 45	1.02 (1.16) 1.26
Trigonostemon magnificus	44 (48.7) 54	39 (44.7) 50	1.02 (1.09) 1.16
Trigonostemon malaccanus	37 (39.6) 41	33 (35.6) 40	1 (1.12) 1.21
Trigonostemon merrillii	35 (41) 49	30 (35.7) 40	1.06 (1.15) 1.3
Trigonostemon murtonii	37 (39.3) 43	32 (35.3) 40	1.08 (1.12) 1.19
Trigonostemon oblongifolius	—	—	—
Trigonostemon pentandrus	45 (47.4) 51	33 (41.6) 46	1.02 (1.15) 1.48
Trigonostemon philippinensis	34 (38.2) 43	30 (35.1) 41	1 (1.09) 1.2
Trigonostemon polyanthus	34 (38.5) 50	27 (31.8) 39	1.03 (1.22) 1.48
Trigonostemon quocensis	40 (44.9) 51	35 (41) 47	1 (1.1) 1.26
Trigonostemon reidioides	34 (38.3) 43	33 (36.1) 41	1 (1.06) 1.14
Trigonostemon rubescens	27 (31.8) 37	24 (30) 36	1 (1.06) 1.14
Trigonostemon rufescens	30 (35.4) 39	28 (28.7) 30	1.07 (1.23) 1.39
Trigonostemon sandakanensis	37 (39.1) 41	35 (37.2) 40	1 (1.05) 1.14
Trigonostemon scopulatus	38 (42) 45	34 (37.7) 41	1.05 (1.12) 1.22
Trigonostemon semperflorens	33 (35.3) 37	31 (32.7) 36	1.03 (1.08) 1.13
Trigonostemon serratus	38 (42.6) 46	30 (37.9) 44	1.02 (1.13) 1.27

Table 1 (cont.)

Species	L (µm)	S (µm)	L/S
Trigonostemon sinclairii	35 (38.7) 42	32 (35.7) 40	1 (1.09) 1.19
Trigonostemon sp. aff. *bonianus*	44 (46.7) 52	37 (40.9) 46	1.02 (1.15) 1.33
Trigonostemon sp. aff. *victoriae*	47 (49.5) 52	45 (46) 47	1 (1.08) 1.16
Trigonostemon stenophyllus	38 (41.4) 45	33 (36.6) 41	1 (1.14) 1.21
Trigonostemon verticillatus var. *salicifolius*	37 (44.3) 51	34 (36.6) 42	1.03 (1.21) 1.43
Trigonostemon verticillatus var. *verticillatus*	43 (46.6) 51	37 (41.6) 47	1.02 (1.12) 1.28
Trigonostemon victoriae	39 (43.8) 47	33 (40.7) 45	1.02 (1.08) 1.18
Trigonostemon villosus var. *borneensis*	—	—	—
Trigonostemon villosus var. *cordatus*	42 (45.9) 50	36 (40.7) 43	1.02 (1.13) 1.25
Trigonostemon villosus var. *merrillianus*	43 (46.4) 49	37 (40.3) 44	1.05 (1.16) 1.3
Trigonostemon villosus var. *villosus*	48 (53.5) 60	42 (46.3) 49	1.02 (1.16) 1.3
Trigonostemon viridissimus var. *elegantissimus*	64 (71) 86	50 (58) 63	1.1 (1.22) 1.4
Trigonostemon viridissimus var. *viridissimus*	45 (53.3) 58	42 (48.8) 56	1 (1.1) 1.28
Trigonostemon wildeorum	41 (48) 56	38 (41.8) 46	1.03 (1.15) 1.33
Trigonostemon wui	41 (44.4) 48	38 (40.8) 47	1.02 (1.09) 1.16
Trigonostemon xyphophylloides	36 (41.4) 49	30 (37) 47	1.04 (1.12) 1.3
Tritaxis gaudichaudii	56 (60.3) 67	50 (55.9) 60	1 (1.08) 1.2

(1a) *Trigonostemon reidioides* type, *reidioides* subtype (Figures 34a–f, 35g, h, 37a, 38a–k', m, m', p, p', s–w')

Tectum reticulate; muri 0.1–0.7 µm wide. Ornamentation: croton pattern; subunits obtuse, triangular to circular from 'above', 0.2–1 µm in diameter, each supported by one or more columellae (Figures 35g, h, 37a), smooth (e.g., *Trigonostemon longipes*; [Figure 34a']) or scabrate (e.g., *T. capillipes* [Figure 34d], *T. detritiferus*, [Figure 34e]); lumina 0.1–1.5 µm in diameter, with granules. Species: *T. aurantiacus*, *T. beccarii*, *T. capillipes*, *T. detritiferus*, *T. dipteranthus*, *T. flavidus*, *T. heteranthus*, *T. longipes*, *T. magnificus*, *T. malaccanus*, *T. murtonii*, *T. philippinensis*, *T. pentandrus*, *T. polyanthus*, *T. reidioides*, *T. rubescens*, *T. rufescens*, *T. scopulatus*, *T. semperflorens*, *T. serratus*, *T. sinclarii*, *T.* sp. aff. *victoriae*, *T. stenophyllus*, *T. verticillatus* (both varieties), *T. victoriae*, *T. villosus* (all four varieties), *T. wildeorum*, *T. xyphophylloides*.

(1b) *Trigonostemon reidioides* type, *longifolius* subtype (Figures 34g–i', 35i, j, 37b, 38l, l', n–o')

Tectum reticulate; muri 0.6–1.3 µm wide. Ornamentation: croton pattern, though not always readily recognisable; subunits spines, 0.1–0.8 µm in diameter, each supported by one or more columellae; lumina 0.6–3.8 µm in diameter, with granules. Species: *T. inopinatus*, *T. longifolius*, *T. merrillii*, *T. oblongifolius*, *T. sandakanensis*.

(2) *Trigonostemon verrucosus* type (Figures 35a–f, k, l, 37c, d, 38q–r', x, x', 39f, f')

Tectum finely reticulate to rugulate; muri 0.2–0.8 µm wide. Ornamentation: verrucate, sometimes almost gemmate; verrucae 0.6–2.5 µm in diameter, obtuse, smooth (e.g., *T. laevigatus*, Figure 35c′, f) or finely rugulate (e.g., *T. capitellatus* [Figure 35a′], *T. cherrieri*,

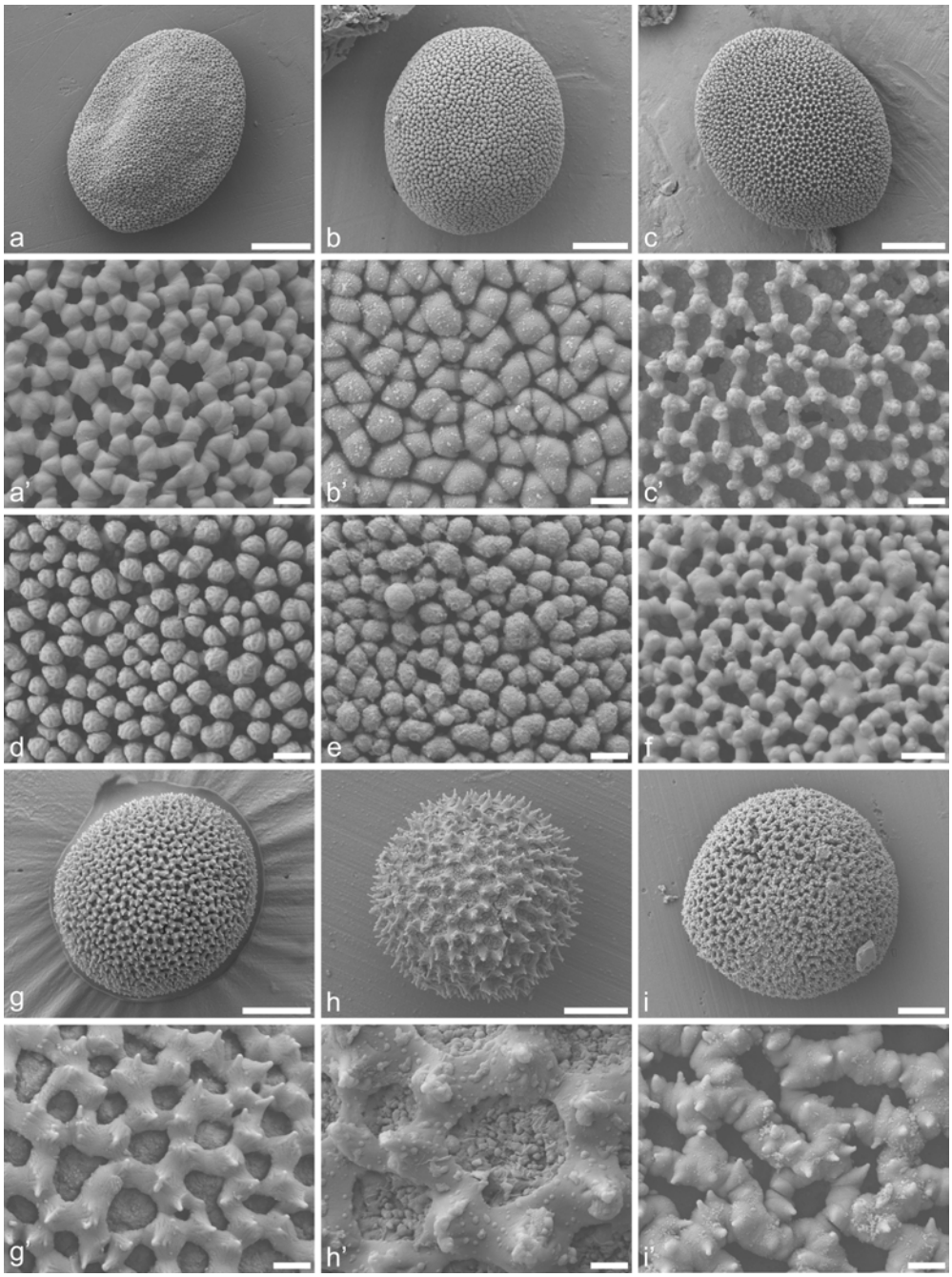


Figure 34 Scanning electron micrographs of the *Trigonostemon reidiodes* pollen type: *reidioides* subtype (a–f) and *longifolius* subtype (g–i′) a, a′. *T. longipes*; b, b′. *T. pentandrus*; c, c′. *T. rubescens*; d. *T. capillipes*; e. *T. detritiferus*; f. *T. heteranthus*; g, g ′. *T. longifolius*; h, h′. *T. sandakanensis*; i, i′. *T. inopinatus*. Scale bars – 10 μm (a–c, g–i), 1 μm (a′–c′, d–f, g′–i′).

Table 2 Pollen (sub)types and selected characters of *Trigonostemon*, *Dimorphocalyx*, *Ostodes*, *Tritaxis* and *Jatropha*.

taxa/pollen (sub)type			exine thickness	tectum	ornamentation	shape and size ('high' x diameter) of ornamentation elements
Trigonostemon	*reidioides* type	*reidioides* subtype	0.7–2 µm	reticulate	croton pattern	subunits triangular to circular from 'above', obtuse, smooth or scabrate	0.3–0.4 x 0.1–1 µm
		longifolius subtype			croton pattern (excl. *T. inopinatus*)	subunits spines	0.3–0.4 x 0.1–0.8 µm
	verrucosus type			finely reticulate to rugulate	verrucate to ± gemmate	verrucae/gemmae circular from 'above', obtuse, smooth or finely rugulate	0.9–1.3 x 0.6–2.5 µm
Dimorphocalyx			2–5 µm	reticulate	croton pattern	subunits triangular to circular from 'above', obtuse, scabrate or 'vertically' striate	3–3.5 x 1.4–2.9 µm
Ostodes			3–3.5 µm	reticulate	croton pattern	subunits circular from 'above', obtuse, smooth to shallowly striate	2.5–3 x 1.4–2.7 µm
Tritaxis			2.5–3 µm	reticulate	croton pattern	subunits circular from 'above', acute, 'vertically' striate,	c. 2 x 1–1.7 µm
Jatropha			3–5 µm	reticulate	croton pattern	subunits triangular to circular from 'above', obtuse; 'vertically' striate	3–4 x 1.6–3.4 µm

Figure 35b′), each supported by a few columellae (Figures 35k, l, 37c, d); lumina up to 0.5 µm (about circular) or up to 1.5 µm (oblong) in diameter. Species: *T. albiflorus*, *T. capitellatus*, *T. cherrieri*, *T. harmandii*, *T. laevigatus* (both varieties), *T. quocensis*, *T.* sp. aff. *bonianus*, *T. viridissimus* (both varieties), *T. wui*.

Dimorphocalyx (Figures 36a–f, 37e, 39a–c')

Pollen grains spheroidal to ellipsoidal monads (L = 45.5–65 µm, S = 42.7–60.9 µm, L/S = 1–1.16), inaperturate. Exine 2–5 µm thick (including subunits of croton pattern); endexine up to 0.3 µm, absent in many places; foot layer thin (≤ 0.1 µm) or not recognisable; infratectal layer up to 1 µm, columellate; tectum indistinctly reticulate; muri 0.3–1 µm thick, 0.5–1.6 µm wide in *Dimorphocalyx cumingii* (Figure 36b, c) and *D. muricatus* (Figure 36e, f), hard to discern in *D. denticulatus*. Ornamentation: croton pattern; subunits triangular to circular from 'above' (Figures 36b, e, 39a, b, c), obtuse to slightly acute, 3–3.5 µm 'high', 1.4–2.9 µm in diameter, each supported by a few columellae (Figures 36c, f, 37e), scabrate in *D. denticulatus* or 'vertically' striate in *D. cumingii* (Figure 36b) and *D. muricatus* (Figure 36e); lumina 1–2.5 µm in diameter, with granules (Figure 36b, e). Species: *D. cumingii*, *D. denticulatus*, *D. muricatus*.

Ostodes (Figures 36g–i, 37f, 39d, d')

Pollen grains spheroidal to ellipsoidal monads (L = 62.7 µm, S = 56.7 µm, L/S = 1–1.19), inaperturate. Exine 3–3.5 µm thick (including subunits of croton pattern); endexine not recognisable; foot layer thin (≤ 0.1 µm); infratectal layer up to 0.5 µm, columellate; tectum indistinctly reticulate; muri up to 0.6 µm thick. Ornamentation: croton pattern; subunits circular to triangular from

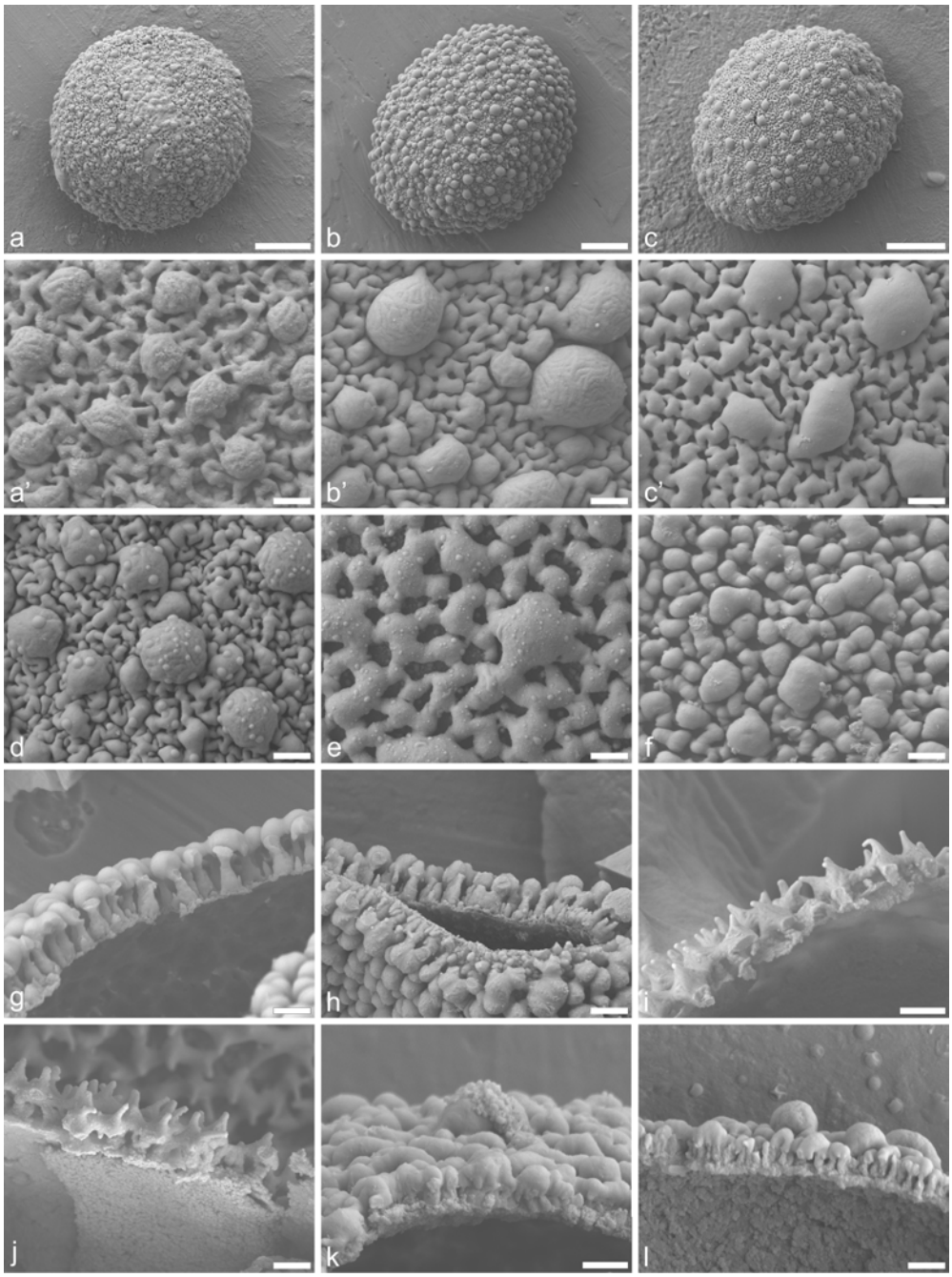


Figure 35 Scanning electron micrographs of the *Trigonostemon verrucosus* pollen type (a–f) and exine cross-sections of the reidiodes type: *reidioides* subtype (g, h), *longifolius* subtype (i, j) and *verrucosus* type (k, l). a, a′. *T. capitellatus*; b, b′. *T. cherrieri*; c, c′. *T. laevigatus* var. *laevigatus*; d. *T.* sp. aff. *bonianus*; e. *T. viridissimus* var. *viridissimus*; f. *T. laevigatus* var. *croceus*; g. *T. dipteranthus*; h. *T. villosus* var. *borneensis*; i. *T. longifolius*; j. *T. oblongifolius*; k. *T. laevigatus* var. *croceus*; l. *T.* sp. aff. *bonianus*. Scale bars – 10 µm (a–c), 1 µm (a′–c′, d–l).

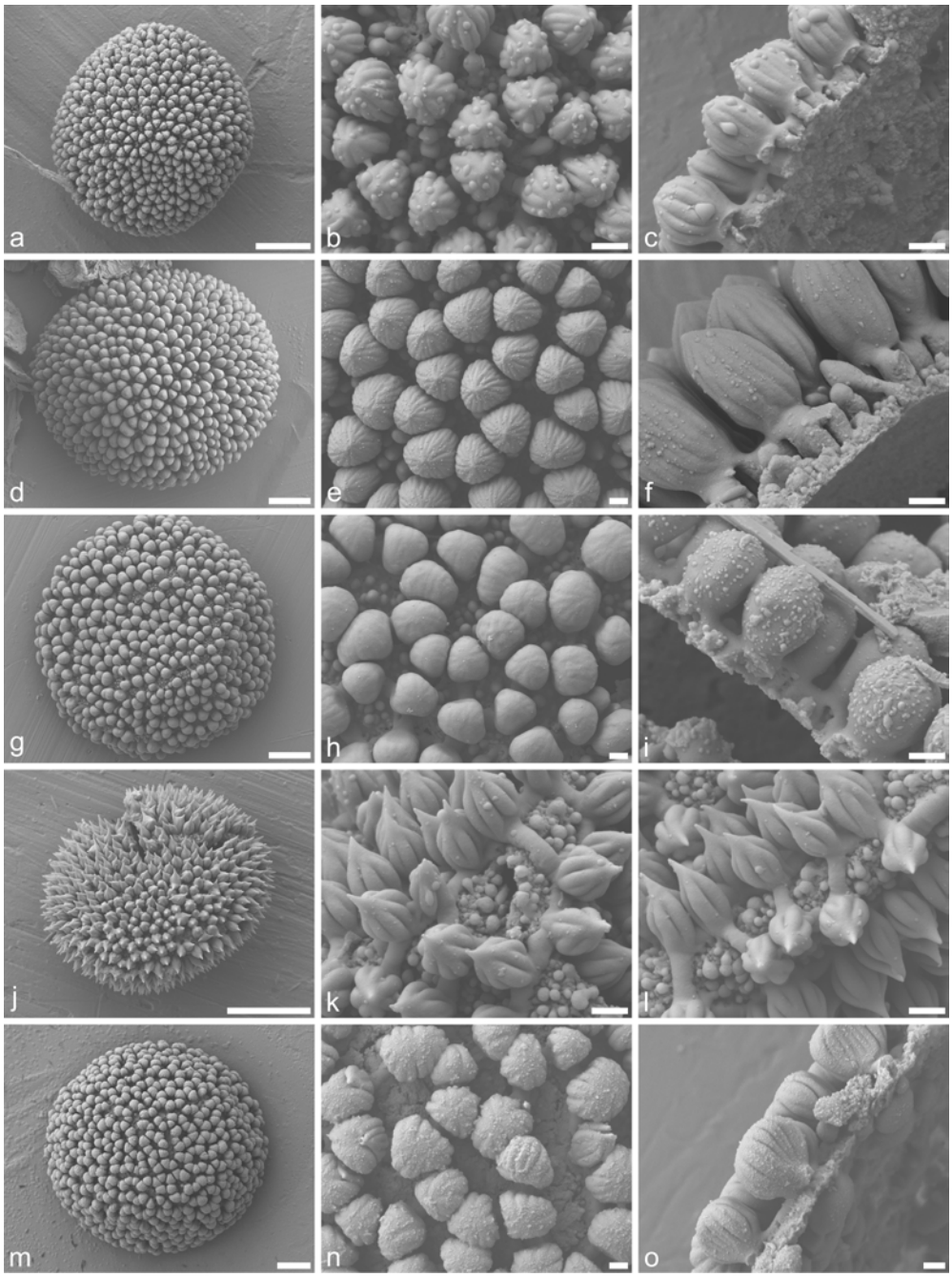


Figure 36 Scanning electron micrographs of the pollen of *Dimorphocalyx*, *Ostodes*, *Tritaxis* and *Jatropha*. a–c. *D. cumingii*. d–f. *D. muricatus*. g–i. *O. paniculata*. j–l. *Tritaxis gaudichaudii*. m–o. *J. multifida*. Scale bars – 10 µm (a, d, g, j, m), 1 µm (b, c, e, f, h, i, k, l, n, o).

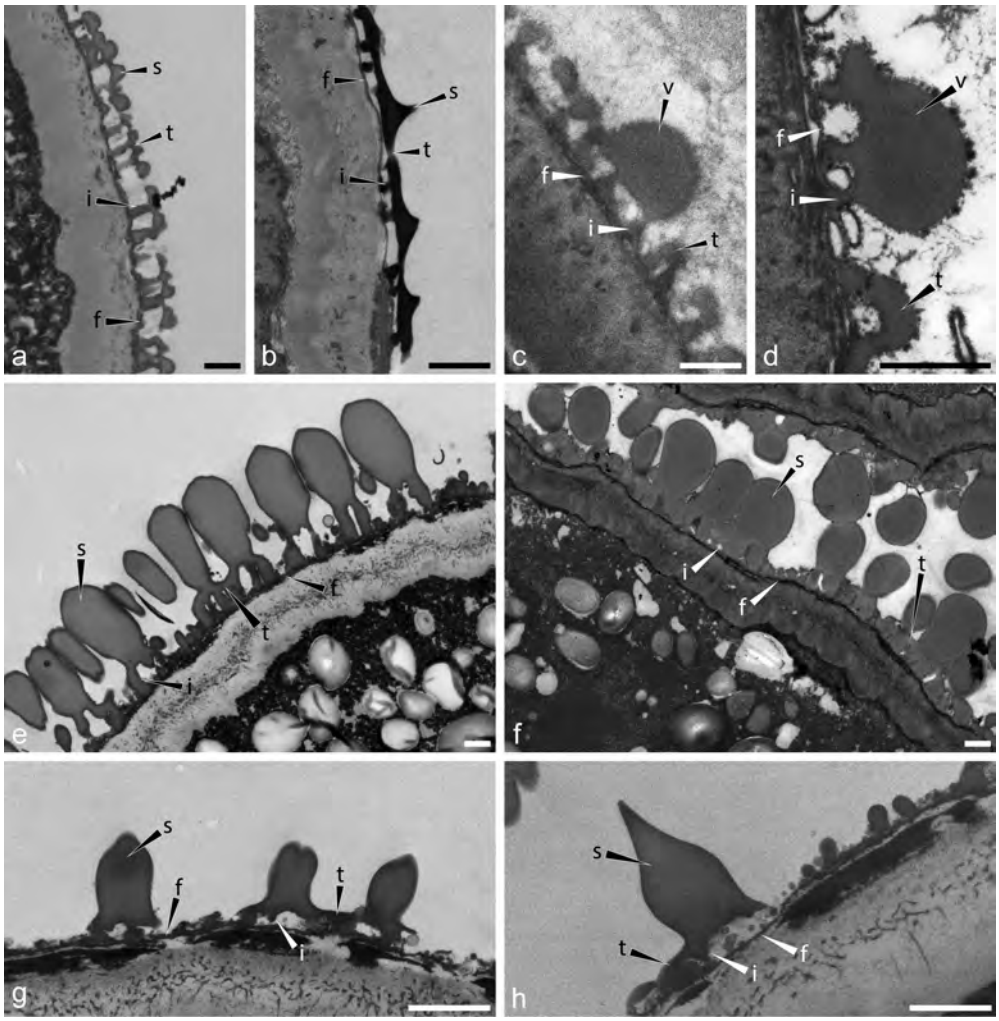


Figure 37 Transmission electron micrographs of pollen exine cross-sections of *Trigonostemon*, *Dimorphocalyx*, *Ostodes* and *Tritaxis*. a. *Trigonostemon verticillatus* var. *verticillatus* (*reidioides* subtype). b. *Trigonostemon longifolius* (*longifolius* subtype). c. *Trigonostemon laevigatus* var. *laevigatus* (*verrucosus* type). d. *Trigonostemon viridissimus* var. *viridissimus* (*verrucosus* type). e. *D. muricatus*. f. *O. paniculata*. g, h. *Tritaxis gaudichaudii*. f = foot layer; i = infratectum; s = subunit of croton pattern ornamentation; t = tectum; v = verruca of verrucate ornamentation. Scale bars – 1 µm.

'above' (Figures 36h, 39d), obtuse, 2.5–3 µm 'high', 1.4–2.7 µm in diameter, each supported by two or three columellae (Figures 36i, 37f), with shallow 'vertically' striate ornamentation (Figure 36h); lumina 1.5–3.3 µm in diameter, with granules (Figure 36h). Species: *Ostodes paniculata* var. *paniculata*.

Tritaxis (Figures 36j–l, 37g, h, 39e, e')

Pollen grains spheroidal to ellipsoidal monads (L = 60.3 µm, S = 55.9 µm, L/S = 1–1.2), inaperturate. Exine 2.5–3 µm thick (including subunits of croton pattern); endexine up to 0.3 µm, absent in many places; foot layer thin (≤ 0.1 µm); infratectal layer up to 0.3 µm, with

indistinct columellae; tectum reticulate; muri 0.3 µm thick, 0.4–0.8 µm wide. Ornamentation: croton pattern; subunits about circular from 'above', c. 2 µm 'high', 1–1.7 µm in diameter, 'vertically' striate, top acute (Figures 36k, l, 37g, h); lumina 1.3–2.5 µm in diameter, with granules. Species: *Tritaxis gaudichaudii*.

Jatropha (Figures 36m–o, 39g–h')

Pollen grains spheroidal to ellipsoidal monads (L = 65.6–88.5 µm, S = 63.1–80.1 µm, L/S = 1–1.17), inaperturate. Exine 3–5 µm thick (including subunits of croton pattern); nexine very thin (Nowicke 1994); infratectal layer c. 1 µm thick, columellate to granular (Nowicke 1994); tectum reticulate; muri c. 0.5 µm thick 0.7–1.1 µm wide, often hard to discern (Figure 36n). Ornamentation: croton pattern; subunits triangular (*Jatropha gossypiifolia*, *J. multifida*, Figure 36n) to circular (*J. curcas*) from 'above', obtuse, 3–4 µm 'high', 1.6–3.4 µm in diameter, 'vertically' striate (Figure 36n, o); lumina 2.1–5.8 µm in diameter, with or without granules (Figure 36n). Species: *J. curcas*, *J. gossypiifolia*, *J. multifida*.

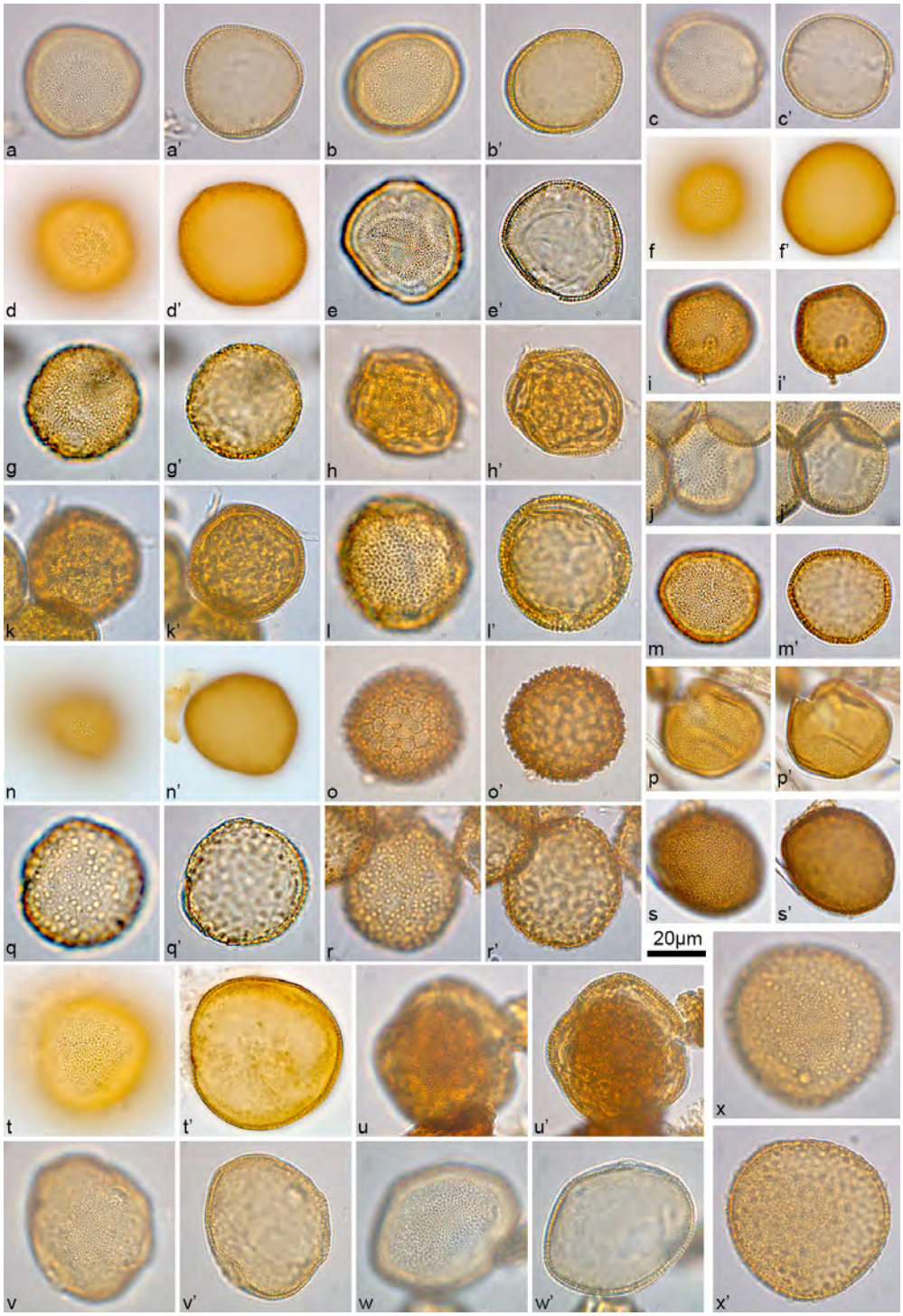
DISCUSSION

The aim of the present pollen study is to gain insight in the infrageneric classification of *Trigonostemon*, and to evaluate the delimitation of this genus against the related genera *Dimorphocalyx*, *Ostodes* and *Tritaxis*. *Jatropha* was added as outgroup and the molecular phylogeny of the uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) of Wurdack et al. (2005) was used to access the polarisation of pollen character states. In the molecular cladogram, *Jatropha* is basal in the C1 branch. This branch is sister to the C2 branch, which includes *Trigonostemon* and *Ostodes*, and supposedly also the closely related genera *Dimorphocalyx* and *Tritaxis*. Together, C1 and C2 make up the 'inaperturate crotonoids', which share the presence of inaperturate pollen with 'croton pattern' ornamentation (Punt 1962; Nowicke 1994; Wurdack et al. 2005). All species in our study possess inaperturate pollen. The croton pattern was found in all five genera, although in a number of *Trigonostemon* species it appeared to be hardly or not recognisable.

Pollen morphology

Agreeing with Punt (1962), two main pollen types based on the presence/absence of the croton pattern ornamentation are distinguished within *Trigonostemon*: (1) the *Trigonostemon reidioides* type (croton pattern, but see later: *Trigonostemon inopinatus*) and (2) the *Trigonostemon verrucosus* type (verrucate to almost gemmate ornamentation). The occurrence of a reticulate tectum with small ornamentation elements (subunits of Nowicke 1994) in the *reidioides* type (Figure 34) and of a finely reticulate to rugulate tectum with larger ornamentation elements in the *verrucosus* type (Figure 35a–f) corroborates this subdivision (see Table 2). In *Trigonostemon heteranthus* the ornamentation is more or less intermediate between the *reidioides* type and the *verrucosus* type. In this species, the croton pattern is recognisable (therefore placed in the *reidioides* type), but locally the subunits are fused to form larger sexine elements reminding of verrucae (Figure 34f).

Based on the shape of the subunits the *reidioides* type can be further divided into two subtypes: (1a) the *reidioides* subtype (subunits obtuse; Figure 34a–f) and (1b) the *longifolius* subtype (subunits spine-shaped; Figure 34g–i). The 'spiny' subunits of the latter subtype differ by their shape, but in both subtypes the subunits have similar dimensions (length, diameter). The croton pattern is not recognisable in *Trigonostemon inopinatus* of the *longifolius* subtype


a
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i
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r
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20µm
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u
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(Figure 34i, i′). In this species, more spines occur and they seem to be randomly placed on the muri of the tectum. Because the spines themselves strongly resemble those of the other species in the *longifolius* subtype, *Trigonostemon inopinatus* is still considered a member of this subtype.

The related genera *Dimorphocalyx*, *Ostodes* and *Tritaxis*, and the outgroup *Jatropha* have similar pollen, all showing large, 'vertically' striate subunits (Figure 36). However, the striate pattern is sometimes shallow (*Ostodes*), or absent, the subunits being irregularly scabrate (*D. denticulatus*). In *Ostodes* and *Jatropha* the subunits are obtuse, in *Dimorphocalyx* obtuse to slightly acute, and in *Tritaxis* clearly acute. The large, 'vertically' striate or scabrate subunits found in these four genera do not occur in *Trigonostemon*, setting this genus apart from the others. Furthermore, the pollen of *Trigonostemon* is relatively small (*reidioides* type: L = 31.8–59.2 µm, *verrucosus* type: L = 39.1–71 µm) compared to that of the other genera: *Dimorphocalyx* (L = 45.5–65 µm), *Ostodes* (L = 62.7 µm), *Tritaxis* (L = 60.3 µm) and *Jatropha* (L = 65.6–88.5 µm). Also, the exine of *Trigonostemon* pollen is thinner than that in the other genera: up to 2 µm versus 2–5 µm (see Table 2).

Pollen and macromorphology

The two pollen types found within *Trigonostemon* correlate well with the macromorphological characters used by Jablonski (1963) to accommodate the (limited number of) species in sections: the degree of division of the stigma lobes and the presence/absence of an appendage on the connective of the stamens. Species belonging to the *reidioides* type have a pistil with deeply divided stigmas (to at least half the length of stigma arm) and stamens with a protruding appendage on the connective, while species of the *verrucosus* type have stigmas that are shortly cleft and stamens without an appendage on the connective. Therefore, it is obvious that pollen characters are useful in the infrageneric classification of *Trigonostemon*. In a future article the pollen types and subtypes and the macromorphological characters will be combined with the results of the molecular analysis (in preparation) in order to propose an infrageneric classification of all species.

As explained earlier, *Trigonostemon inopinatus* is included in the *reidioides* pollen type (*longifolius* subtype), although the 'spiny' subunits do not show the croton pattern (Figure 34i, i′). Macromorphologically, it would fit better in the group of species showing the *verrucosus* type, because the connective of the anther lacks an appendage. However, its pollen does not show verrucate ornamentation. Here, the results of the molecular analysis will be especially interesting. Geographically, *Trigonostemon inopinatus* is also remarkable: it is an endemic and the only *Trigonostemon* species in north Australia; it marks the southern boundary of the distribution area of the genus.

Dimorphocalyx, *Tritaxis* and *Ostodes* are macromorphologically close to *Trigonostemon*, differing in having more stamens in two or more whorls. *Dimorphocalyx* and *Tritaxis* were

Figure 38 Light micrographs of pollen grains of *Trigonostemon*. The first of each set of two micrographs of a species represents an upper focus view, the second a middle focus view. a, a'. *T. capillipes*. b, b'. *T. malaccanus*. c, c'. *T. aurantiacus*. d, d'. *T. pentandrus*. e, e'. *T. polyanthus*. f, f'. *T. flavidus*. g, g'. *T. reidioides*. h, h'. *T. scopulatus*. i, i'. *T. heteranthus*. j, j'. *T. philippinensis*. k, k'. *T. sinclairii*. l, l'. *T. longifolius*. m, m'. *T. rubescens*. n, n'. *T. merrillii*. o, o'. *T. sandakanensis*. p, p'. *T. semperflorens*. q, q'. *T. laevigatus* var. *laevigatus*. r, r'. *T. quocensis*. s, s'. *T. serratus*. t, t'. *T. detritiferus*. u, u'. *T. magnificus*. v, v'. *T. verticillatus* var. *verticillatus*. w, w'. *T. villosus* var. *villosus*. x, x'. *T. viridissimus* var. *viridissimus*. All micrographs are at the same scale. Scale bar – 20 µm.

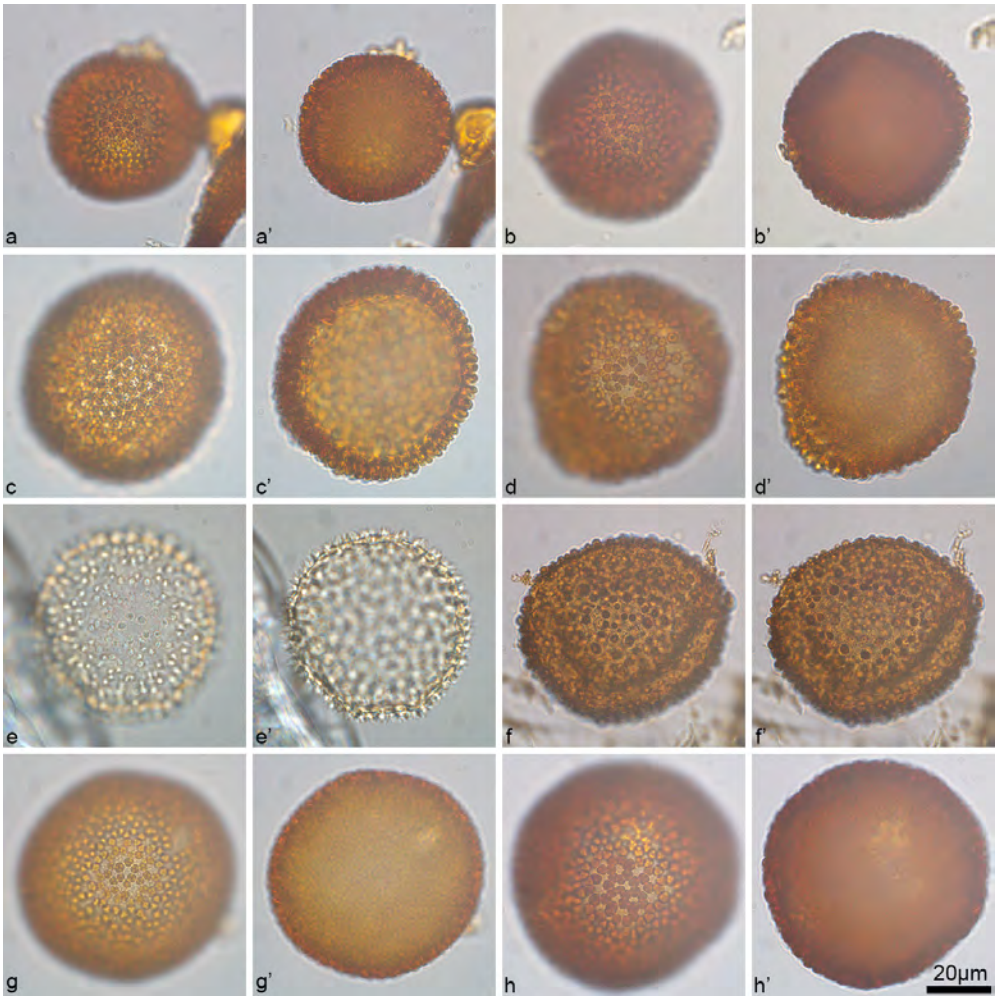

Figure 39 Light micrographs of pollen grains of *Dimorphocalyx*, *Ostodes*, *Tritaxis*, *Trigonostemon* and *Jatropha*. The first of each set of two micrographs of a species represents an upper focus view, the second a middle focus view. a, a'. *D. cumingii*. b, b'. *D. denticulatus*. c, c'. *D. muricatus*. d, d'. *O. paniculata* var. *paniculata*. e, e'. *Tritaxis gaudichaudii*. f, f'. *Trigonostemon cherrieri*. g, g'. *J. gossypiifolia*. h, h'. *J. multifida*. All micrographs are at the same scale. Scale bar – 20 µm.

treated in the genus *Trigonostemon*, though under different generic definitions (see Introduction section; e.g., Müller Argoviensis 1865; 1866; van Welzen & van Oostrum 2015; Yu & van Welzen 2018). Pollen morphology (exine ornamentation and thickness; see earlier) evidently sets *Trigonostemon* apart from *Dimorphocalyx*, *Ostodes* and *Tritaxis*, and the acute top of the subunits of the croton pattern suggests that *Dimorphocalyx* resembles *Tritaxis* more than *Ostodes*.

Dimorphocalyx cumingii, a macromorphologically problematic species with two whorls of a few stamens, is difficult to accommodate in either *Trigonostemon* or one of the other genera. The species was treated in the genus *Trigonostemon* (Müller Argoviensis 1865; 1866; van Welzen & van Oostrum 2015; but under different generic definitions of the genus), *Dimorphocalyx* (Airy

Shaw 1969, 1983b) and even *Tritaxis* (Bentham 1878; Pax 1910; Merrill 1923). The present pollen study (Figure 36a–c) shows that it resembles *Dimorphocalyx* more than *Trigonostemon*.

Phylogenetic considerations

Relatively large pollen grains with 'vertically' striate subunits are shared by many genera of inaperturate crotonoids (Nowicke 1994). These genera are spread over both the C1 (e.g., *Croton*, *Joannesia* and *Jatropha*) and C2 branch (e.g., *Pausandra*, *Ricinocarpus*, *Crotonogyne* and *Paracroton*) of the Euphorbiaceae backbone phylogeny (Wurdack et al. 2005). The species *Ostodes zeylanica* (Thwaites) Müll.Arg. used in Nowicke (1994) is a synonym of *Paracroton pendulus* (Hassk.) Miq. subsp. *zeylanicus* (Thwaites) N.P.Balakr. & Chakrab., see van Welzen and Winkel (2015). These characters also occur in the outgroup (*Jatropha*) and part of the ingroup used in this study (*Dimorphocalyx*, *Ostodes* and *Tritaxis*) and this implies that these character states are pleisiomorphic and therefore cannot be used to draw any conclusions about the mutual relationships of these genera. However, *Trigonostemon* deviates in all these characters from *Jatropha* and other groups studied, which makes its character states of both pollen types derived.

In terms of the 'croton pattern' ornamentation itself, the character is common among the 'inaperturate crotonoids' (both C1 and C2 groups, see earlier), but the *longifolius* subtype shows a modification (a reduction? of the subunits, from obtuse to 'spiny') in the character, and the *verrucosus* type even displays a total loss of the 'croton pattern'. Therefore, these character states are considered apomorphic. If *Trigonostemon inopinatus* is correctly placed in the *longifolius* subtype, then its features are further apomorphies within this subtype. The future results from the molecular studies (in preparation) will enable us to evaluate these considerations.

CONCLUSIONS

Trigonostemon, *Dimorphocalyx*, *Ostodes*, *Tritaxis* and *Jatropha* fit well in the inaperturate crotonoid clade. The *Trigonostemon* species differ from the other four genera by, among other characters, the absence of 'vertically' striate ornamentation on the subunits.

Two pollen types are recognised within *Trigonostemon* based on the presence/absence of the croton pattern ornamentation: (1) the *reidioides* type and (2) the *verrucosus* type, and two subtypes within the former based on the shape of the subunits: (1a) the *reidioides* subtype (subunits obtuse) and (1b) the *longifolius* subtype (subunits 'spiny'). The pollen types correlate well with the macromorphology of the genus: species with the *reidioides* type have deeply divided stigmas and a protruding appendage on the connective, whereas the species with the *verrucosus* type have shortly divided stigmas and connective without an appendage.

Trigonostemon inopinatus (belonging to the *longifolius* subtype) and the species included in the *verrucosus* type differ from the inaperturate crotonoids, because the croton pattern ornamentation, is not recognisable. Possibly, their ornamentation character states are unique within the inaperturate crotonoids clade, suggesting that these pollen character states of the belonging species are derived.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Specimens investigated

LM: n = number of pollen grains examined under; if nothing is mentioned then ten grains were examined. SEM: * = not acetolysed.

Dimorphocalyx cumingii (Müll.Arg.) Airy Shaw: Philippines, *Cumming 1693* (L 0016166), 1837. LM, SEM.

D. denticulatus Merr.: Sarawak (Borneo), *S* (*I. bin Paie*) *22904* (L.2204243), 31 March 1965. LM, SEM.

D. muricatus (Hook.f.) Airy Shaw: Sabah (Borneo), *SAN* (*Madani* et al.) *133913* (L.2204259),14 April 1992. LM, SEM, TEM.

Jatropha curcas L.: Sulawesi, *Chin 3582* (L.2236351), 15 June 1986. LM, SEM.

J. gossypiifolia L.: Caribbean, *Stoffer 1453* (U.1257436), December 1953. LM, SEM.

J. multifida L.: Micronesia, *Stone 4047* (L.2236090), 9 April 1962. LM, SEM.

Ostodes paniculata Blume var. *paniculata*: Thailand, *Phusomsaeng 407* (L.2255389), 26 March 1968. LM, SEM, TEM.

Trigonostemon albiflorus Airy Shaw: Vietnam, *Gillespie* et al. *7405* (L.2260160), 11 April 2005. LM, SEM.

Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl.: Thailand, *Maxwell 87-566* (L.2260177), 14 June 1987. LM (n = 5), SEM.

Trigonostemon beccarii Ridl.: Sumatra, *Achmad 1773* (L.2260147), 2 April 1920. LM (n = 6), SEM.

Trigonostemon capillipes (Hook.f.) Airy Shaw: Thailand, *Geesink & Santisuk 4961* (L.2258613), 26 April 1973. LM, SEM.

Trigonostemon capitellatus Gagnep.: Java, *Bogor Botanical Garden VIII.E.16* (L.2258669), LM; Alston 17134 (L.2258671), 23 September 1954. LM, SEM*.

Trigonostemon cherrieri J.M.Veillon: New Caledonia, *Veillon 7385* (L 0016479), 25 June 1991. LM, SEM.

Trigonostemon detritiferus R.I.Milne: Brunei (Borneo), *R.Y. Yu 102*, 14 October 2016. LM, SEM.

Trigonostemon dipteranthus Airy Shaw: Sumatra, *Korthals s.n.* (L.2260569), 1833 or 1836. LM, SEM.

Trigonostemon flavidus Gagnep.: China, *R.Y. Yu 264*, 13 July 2018. LM, SEM.

Trigonostemon harmandii Gagnep.: Laos, *Poilane 20983* (L.2260524), 1 April 1932. LM, SEM.

Trigonostemon heteranthus Wight: Thailand, *Kerr 20367* (L.2260551), 5 March 1931. LM (n = 6), SEM.

Trigonostemon inopinatus Airy Shaw: Queensland, Australia, *Hyland 8176* (L.2260534), 7 May 1975. LM, SEM.

Trigonostemon laevigatus Müll.Arg. var. *croceus* R.Y.Yu & Welzen: Malay Peninsula, *Chin 3373* (L.2260552), 26 August 1986. LM, SEM.

Trigonostemon laevigatus Müll.Arg. var. *laevigatus*: East Kalimantan (Borneo), *Ambriansyah & Arifin 714* (L.2260506), 13 April 1991. LM, SEM, TEM.

Trigonostemon longifolius Wall. ex Baill.: Thailand, *Maxwell 86-322* (L.2260463), 1 June 1986, LM; Sabah, *Elmer 20936* (L 0160141), October 1922. SEM, TEM.

Trigonostemon longipes (Merr.) Merr.: Philippines, *BS* (*M. Ramos & G.E. Edaño*) *34041* (L.2260414), February 1919. LM, SEM.

Trigonostemon magnificus R.I.Milne: Sumatra, *de Wilde & de Wilde-Duyfjes 19441* (L.2260380), 6 August 1979. LM, SEM.

Trigonostemon malaccanus Müll.Arg.: Malay Peninsula, *Griffith s.n.* (L 0016481). LM, SEM.

Trigonostemon merrillii Elmer: Philippines, *R.Y. Yu 255*, March 2018. LM, SEM.

Trigonostemon murtonii Craib: Cambodia, *WA* (*Webb* et al.) *207* (L.2260393), 24 February 2003. LM (n = 3), SEM.

Trigonostemon oblongifolius Merr.: Philippines, *BS* (*Curran*) *19604* (L 0160281), January, 1912. SEM.

Trigonostemon pentandrus Pax & K.Hoffm.: Malay Peninsula, *FRI* (*R.Y. Yu & Angan*) *86651*, 16 December 2016. LM, SEM.

Trigonostemon philippinensis Stapf: Sumatra, *Ramat Si Boeea 9870* (L.2258730), 1 August 1936. LM, SEM.

Trigonostemon polyanthus Merr.: Philippines, *BS* (*Ramos*) *1645* (L.2258801), April 1914. LM, SEM*.

Trigonostemon quocensis Gagnep.: Thailand, *Maxwell 76-334* (L.2258809), 9 May 1976. LM, SEM.

Trigonostemon reidioides (Kurz) Craib: Laos, *Maxwell 98-97* (L.2258767), 1 February, 1998. LM, SEM.

Trigonostemon rubescens Gagnep.: Thailand, *Geesink* et al. *6514* (L.2258772), 3 May 1974. LM, SEM.

Trigonostemon rufescens Jabl.: Malay Peninsula, *FRI* (*R.Y. Yu & Angan*) *86664*, 18 December 2016. LM, SEM.

Trigonostemon sandakanensis Jabl.: Sabah (Borneo), *Sinclair* et al. *9308* (L.2258762), 28 June 1957. LM, SEM.

Trigonostemon scopulatus R.Y.Yu & Welzen: Malay Peninsula, (*KEP*) *FRI* (*Cockburn*) *7859* (L.2258747), 22 March 1968. LM, SEM.

Trigonostemon semperflorens (Roxb.) Müll.Arg.: India, *Koelz 27971* (L.2258763), 9 May 1951. LM, SEM.

Trigonostemon serratus Blume: Java, *Blume 1648* (L.2258713), 1821–1825. LM, SEM.

Trigonostemon sinclairii Jabl.: Malay Peninsula, (*KEP*) *FRI* (*Chan*) *23976* (L.2258561), 3 August 1977. LM, SEM.

Trigonostemon sp. aff. *bonianus* Gagnep.: India, *Koelz 27903* (L.2260526), 6 May 1951. LM (n = 4), SEM.

Trigonostemon sp. aff. *victoriae*: Philippines, *R.Y. Yu 260*, April 2018. LM (n = 2), SEM

Trigonostemon stenophyllus Quisumb.: Philippines, *R.Y. Yu 242*, March 2018. LM, SEM.

Trigonostemon verticillatus (Jack) Pax var. *salicifolius* (Ridl.) Whitmore: Malay Peninsula, *Worthington 13073* (L.2258554), 19 July 1987. LM, SEM.

Trigonostemon verticillatus (Jack) Pax var. *verticillatus*: Malay Peninsula, (*KEP*) *FRI* (*Julius* et al.) *54879* (L.3799339) 31 January 2007. LM, SEM, TEM.

Trigonostemon victoriae R.Y.Yu & Welzen: Philippines, *R.Y. Yu 258*, April 2018. LM, SEM.

Trigonostemon villosus Hook.f. var. *borneensis* (Merr.) Airy Shaw: Sumatra, *de Wilde & de Wilde-Duyfjes 21244* (L.2258571), 31 August 1991. SEM.

Trigonostemon villosus Hook.f. var. *cordatus* R.Y.Yu & Welzen: Sabah (Borneo): *SAN* (*R.Y. Yu* et al.) *158479*, 11 December 2016. LM, SEM.

Trigonostemon villosus Hook.f. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen: Philippines, *R.Y. Yu 254*, March 2018. LM, SEM.

Trigonostemon villosus Hook.f. var. *villosus*: Malay Peninsula, (*KEP*) *FRI* (*Vethevelu*) *29673* (L.2260365), 5 May 1982. LM (n = 8), SEM.

Trigonostemon viridissimus (Kurz) Airy Shaw var. *elegantissimus* (Airy Shaw) Airy Shaw: East Kalimantan (Borneo), *Kostermans 13695* (L.2258606), 3 September 1957. LM (n = 6), SEM.

Trigonostemon viridissimus (Kurz) Airy Shaw var. *viridissimus*: Lesser Sunda Islands, *van Steenis 18211* (L.2258598), 20 December 1953. LM, SEM, TEM.

Trigonostemon wildeorum R.Y.Yu & Welzen: Sumatra, *de Wilde & de Wilde-Duyfjes 18742* (L.2258573), 16 July 1979. LM.

Trigonostemon wui H.S.Kiu: China, *R.Y. Yu 266*, 13 July 2018. LM (n = 8), SEM.

Trigonostemon xyphophylloides (Croizat) L.K.Dai & T.L.Wu: China, *R.Y. Yu 265*, 13 July 2018. LM (n = 8).

Tritaxis gaudichaudii (Baill.) Müll.Arg.: Vietnam, *Soejarto* et al. *14143* (L.3784654), 5 July 2008. LM, SEM, TEM.

Chapter 6 Molecular Phylogeny of *Trigonostemon* and its relatives (Euphorbiaceae)

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Abstract *Trigonostemon*, *Dimorphocalyx*, *Tritaxis* and *Ostodes* are tropical Asian genera that are very similar in morphology. The former three genera have been treated either as a single genus *Trigonostemon sensu lato* or as separate genera. A molecular phylogeny based on the nuclear ITS and chloroplast *trnK* intron, *trnT-L* and *trnL-F* sequences reveals that *Trigonostemon* is a monophyletic group, and *Dimorphocalyx* and *Tritaxis* together form another monophyletic group separate from *Trigonostemon*. Within the genus *Trigonostemon* a strong correlation between the molecular phylogeny and pollen morphology is found. It demonstrates two potential evolutionary directions for the common 'croton pattern' ornamentation of pollen in the genus: the subunits that form the 'croton pattern' ornamentation tend to reduce to spines or they tend to merge together in the later developed groups. The correlation between the molecular phylogeny and macromorphology of *Trigonostemon* is discussed and a new infrageneric classification with four sections is provided. *Dimorphocalyx* is reduced to *Tritaxis*, the older generic name.

Key words

Dimorphocalyx
Euphorbiaceae
Ostodes
phylogeny
pollen
taxonomy
Trigonostemon
Tritaxis

INTRODUCTION

Trigonostemon Blume is a genus in the Euphorbiaceae containing about 60 species of monoecious small trees or shrubs growing in lowland rainforests. The plants are found from S India and Sri Lanka to S China, throughout continental SE Asia and Malesia to NE Australia and the W Pacific (Govaerts et al. 2000). The genus is morphologically recognised by the 5-merous flowers with colourful petals (purple, red, pink, orange, yellow, white and intermediate colours between these) and one whorl of three or five connate stamens (Figure 40a–f).

Trigonostemon is traditionally classified in the subfamily Crotonoideae, tribe Codiaeae, subtribe Trigonostemoniae (Webster 2014). In the molecular phylogeny of the uniovulate Euphorbiaceae (Wurdack et al. 2005) it is placed in the C2 clade of the subfamily Crotonoideae, close to *Ostodes* Blume and other genera.

Blume (1825) established the genus based on *Trigonostemon serratus* Blume, which has one whorl of three connate stamens forming a triangular shape when seen from 'above', hence the generic name. After Blume, over 140 scientific names were published within *Trigonostemon* (Govaerts et al. 2000), although the circumscription of the genus has remained unclear during the years. The previous studies diverged into two mainstream opinions: (1) Müller Argoviensis (1865, 1866), as opposed to Blume's (1825) original definition, regarded the genus in a wider sense by including species with two or three whorls of stamens in *Trigonostemon*; as a result, a few genera including *Dimorphocalyx* Thwaites (1861; two whorls of stamens, Figure 40k) and *Tritaxis* Baillon (1858; three whorls of stamens, for illustration see Gagnepain 1925b) were merged with *Trigonostemon* into a new *Trigonostemon sensu lato*; (2) most other botanists, e.g., Bentham (1878, 1880) and Pax (1890), preferred Blume's concept (1825), keeping *Trigonostemon* restricted to the species with only one whorl of stamens. Airy Shaw (1969) had an eclectic opinion between the two theories. He kept *Dimorphocalyx* separate but included *Tritaxis* in *Trigonostemon* despite the 13 stamens of *Tritaxis* being obviously aberrant among the other species. Unfortunately, none of these circumscriptions has yet been confirmed by a molecular phylogeny. In addition, *Ostodes* has 20–41 stamens, with the inner ones partly connate (van Welzen & Winkel 2015; Figure 40l), suggesting a potentially close relationship with *Trigonostemon* and *Dimorphocalyx*. Therefore, *Ostodes* should also be taken into account when assessing this whole complex. All these genera have petals in the pistillate flowers, which make them distinct from most other Euphorbiaceae.

Within *Trigonostemon sensu stricto*, a few infrageneric classifications have been made using different combinations of morphological characters (for a brief review, see Yu & van Welzen 2018): Bentham (1878, 1880) and Hooker (1887) emphasised the position of the inflorescences, the number and division of the anthers, and they designated three sections within the genus; Merrill (1924) and Pax & Hoffmann (1931) extended this system to include five sections; Jablonski (1963) did not rely on the number of stamens but focused on whether the stigmas were bifid or not, and recognised three sections (only for the species of the Malay Peninsula, Sumatra and Borneo). Unfortunately, these classifications are not generally applicable, because they were based on a limited number of species and contained confusing misidentifications and misplacements.

At present the main genera involved in the complex, i.e., *Trigonostemon*, *Dimorphocalyx* and *Ostodes*, are already morphologically revised for the Flora Malesiana project (Yu & van Welzen 2018; van Welzen & van Oostrum 2015; van Welzen & Winkel 2015, respectively) and other local floras (e.g., Chakrabarty & Balakrishnan 1990, 1993; Balakrishnan & Chakrabarty

1991; Chantaranothai 2007; Phattarahirankanok & Chayamarit 2005, 2007; Li & Gilbert 2008). Six species have been treated within *Tritaxis* in the literature (also see Taxonomic treatment below), but these names are now all synonymised within *Trigonostemon* (Airy Shaw 1969, Yu & van Welzen 2018), *Dimorphocalyx* (van Welzen & van Oostrum 2015) and *Paracroton* Miq. (Balakrishnan & Chakrabarty 1993, Esser 2007). Additionally, the pollen morphology of all these genera was also studied (Yu et al. 2019c). Two major pollen types (including two subtypes; Figure 40m–t) were found in *Trigonostemon* (sensu Blume 1825), but the pollen characters could not yet be discussed in the light of evolution because a phylogeny was still lacking. Therefore, the aim of our study is to analyse the phylogenetic relationships between *Trigonostemon* and its closely resembling genera using several molecular markers (nuclear ITS and the chloroplast *trnK* intron, *trnT-L*, *trnL-F* and *rbcL*), in order to (1) confirm the systematic position of *Trigonostemon* in the family, (2) clarify the generic delimitation of *Trigonostemon* and its possible relatives, (3) interpret the evolutionary trends in *Trigonostemon* in reference to the pollen morphology and (4) revise the infrageneric classification of the genus.

MATERIAL AND METHODS

Leaf samples of 41 species (out of about 60, Yu & van Welzen 2018) and four varieties of *Trigonostemon*, 11 species (out of about 13, van Welzen & van Oostrum 2015) of *Dimorphocalyx*, one species (probably monotypic, Gagnepain 1925b) of *Tritaxis*, one species (out of two, van Welzen & Winkel 2015) of *Ostodes* and one species of *Jatropha* L. (used as outgroup; selection based on Wurdack et al. 2005, for details see discussion) were used in the analysis. *Trigonostemon* is here regarded in the strict sense (see Introduction) and *Tritaxis* is taken separately, not as part of *Trigonostemon*. The samples were collected in the field (dried in silica gel) or taken from herbarium collections. Taxa and voucher information are shown in Table 3.

Total genomic DNA was isolated from fresh and herbarium materials using the standard CTAB extraction protocol (Doyle & Doyle 1987).

The nuclear ribosomal internal transcribed spacer (nrITS) and chloroplast *trnK* intron, *trnT-L*, *trnL-F* (including the *trnL* intron and *trnL-F* spacer) and *rbcL* (of only a few species, see Table 3) were amplified from genomic DNA using the polymerase chain reaction (PCR). The primer information is shown in Table 4.

The PCR was performed with the following reaction components: 10–100 ng genomic DNA, 5µl 5x PCR buffer (containing 15 mM $MgCl_2$; Thermo Fisher, Waltham, USA), 1µl bovine serum albumin (BSA; Life),1µl dNTPs, 1µl for both forward and reverse primers in 10 µM and 2.5 U *Taq* DNA polymerase (Thermo Fisher, Waltham, USA) and adjusted to a final volume of 25 µl by ultrapure water. The PCR program was: initialization at 98°C for 2.5 minutes, followed by 35–40 cycles of denaturation: 98°C for 15 seconds, annealing: 48–55°C for 15 seconds, extension: 72°C for 45–60 seconds, followed by a final extension for 5 minutes and eventually stopped at 12°C as a final hold. The PCR products were sequenced at BaseClear, Leiden, the Netherlands. The sequencing results were aligned using Geneious 8.1.8 (https://www.geneious.com) with the multiple sequence Geneious alignment algorithm and then manually adjusted within the same program. Some sequences were trimmed at the two ends to reduce missing data. Two matrices were made. In matrix 1 all sequences obtained from this study were aligned with the dataset of the Euphorbiaceae based on *trnL-F* and *rbcL* sequences (Wurdack et al. 2005); in total 5 markers were used: the nuclear ITS and the chloroplast *trnK* intron, *trnT-L*, *trnL-F* and *rbcL*. Matrix 2 included the nuclear ITS and the chloroplast *trnK* intron, *trnT-L* and *trnL-F* sequences for a restricted dataset of *Trigonostemon* and allies.

Figure 40 Illustrations of the key characters of *Trigonostemon*, *Dimorphocalyx* (now *Tritaxis*) and *Ostodes*. a. staminate flower, showing the divaricate stamens (*Trigonostemon pentandrus*); b. staminate flower, showing the non-divaricate stamens (*T. albiflorus*); c. androphore, showing the divaricate stamens and disc lobes (*T. philippinensis*); d. androphore, showing the non-divaricate stamens and an annular disc (*T. viridissimus* var. *viridissimus*); e. pistillate flowers, showing the deeply bifid stigmas (*T. filiformis*); f. pistillate flowers, showing the stigmas only very slightly bifid at apex (*T. albiflorus*); g. pistil, showing the deeply bifid stigmas and disc lobes (*T. villosus* var. *merrillianus*); h. top of a pistil, showing the stigmas only very slightly bifid at apex (*T. viridissimus* var. *elegantissimus*); i. young fruits, showing the non-accrescent sepals (*T. longipes*); j. a young fruit, showing the accrescent sepals (*T. victoriae*); k. staminate flowers of *Dimorphocalyx ixoroides* [= *Tritaxis ixoroides*];

The phylogenetic trees were reconstructed separately based on the two alignments under Maximum Parsimony (MP; matrices 1 and 2) using PAUP 4.a165 (Swofford 2002), Maximum Likelihood (ML; only matrix 2) using RaxML 8.2.10 and Bayesian Inference (BI; matrices 1 and 2) using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001). The analyses were performed via the CIPRES Science Gateway (Miller et al. 2010; http://www.phylo.org/). In order to minimize bias in the comparison of results, analyses based on matrix 1 (MP and BI) were performed under the same parameters as Wurdack et al. (2005); the settings for analyses of matrix 2 were as follows:

In the MP analysis, all nucleotide characters were treated unordered and unweighted, polymorphisms were treated as uncertainties and gaps were treated as missing data. The heuristic search for the most parsimonious trees was performed using the tree-bisection-reconnection (TBR) swapping algorithm on starting trees obtained by a 1,000 random taxon additional sequence replicates (RAS), holding 10 trees at each step, with an unlimited maximum number of trees to be saved. The 50% majority consensus tree was calculated. A bootstrap analysis (Felsenstein 1985) of 5,000 replicates was made to evaluate the support for the clades, where each replicate of RAS (= 100) and TBR (holding 10 trees at each step) had a limit of maximum 100 trees saved.

The ML tree was reconstructed under General Time Reversible (GTR) model (Nei & Kumar 2000). A discrete Gamma distribution (+Γ) was used to model evolutionary rate differences among sites (4 categories), and a certain fraction of sites are assumed evolutionarily invariable (+I). 100,000 replicates of bootstrap analysis were performed.

The BI analyses were conducted with two independent runs of four Markov-Monte Carlo chains (MCMC), using the General Time Reversible (GTR+Γ+I) model (Nei & Kumar 2000) for a total of 100,000,000 generations. After every 1,000 generations a tree was sampled and the first 25% trees were discarded as burn-in. In the ML and BI analysis, the substitution model was selected based on the lowest Akaike Information Criterion scores detected by Modeltest-NG 0.1.5 (Darriba et al. 2019).

RESULTS

Sequence alignments

Sequences of 62 taxa were obtained. There are relatively fewer taxa with chloroplast sequences than those with ITS because of failure in PCR. Particularly, the amplifications of the *trnK* intron and *trnT-L* failed more often in *Dimorphocalyx* species. Properties of the sequences are shown in Table 5. Because the nuclear ITS and chloroplast *trnK* intron and *trnT-L* sequences were not included in Wurdack et al. (2005), the alignments of these three markers are the same in both matrices.

The aligned ITS sequences contain 693 nucleotide sites, of which 311 are variable and 169 are parsimony informative. The non-coding parts (ITS1 and ITS2) present most variation.

←

l, staminate flowers of *Ostodes paniculata*; m, n. *T. reidioides* type and *T. reidioides* subtype pollen (*T. reidioides*); o, p. *T. reidioides* type *T. longifolius* subtype pollen (*T. sandakanensis*); q, e. *T. verrucosus* type pollen (*T. laevigatus* var. *laevigatus*); s, t. Pollen of *T. inopinatus*. Photos a–j by Ren-Yong Yu; photo k © P.B. Pelser & J.F. Barcelona (Pelser et al. 2011 onwards); photo l © N. Pattharahirantricin, reproduced with permission from the Editorial Board of the Flora of Thailand project; Photos m–t by Ren-Yong Yu, reproduced from Grana 58: 114–128.

Table 3 Voucher information. * = cultivated. *Trigonostemon* sp. 1 will be described as *T. palustris* R.Y.Yu & Welzen (Yu et al. 2019a); *Trigonostemon* sp. 2 will be described as *T. montanus* R.Y.Yu & Welzen (2019b); we were unable to identify *Trigonostemon* sp. 3 for the time being.

Taxa	Collector	Field No.	Location	Barcode	ITS	*trnK* intron	*trnT-L*	*trnL-F*	*rbcL*
Dimorphocalyx australiensis	Gray	7859	Australia	L.2211804	MK876508	MK876670	MK876568	MK876614	
D. beddomei	Ridsdale	388	India	L.2211814	MK876509	MK876671		MK876615	
D. cumingii	Mendoza	PNH 42406	Philippines	L.2211815	MK876519				
D. denticulatus	Church	1819	W. Kalimantan	L.2204228	MK876510	MK876672		MK876616	
D. glabellus	Kosterman	26317	India	L.2204358	MK876511			MK876617	
D. ixoroides	Ruffo	PNH 41828	Philippines	L.2204362	MK876512			MK876618	
D. malayanus	Sidisunthorn	ST 1640	Thailand	L.2204317	MK876513			MK876619	
D. moluccensis	Ramlanto	905	Moluccas	L.2204173				MK876620	
D. muricatus	Pooma	4499	Thailand	L.2204330	MK876514			MK876621	
D. pauciflorus	Forman	906	Brunei	L.2211818	MK876516				
D. sp.	Yu	SAN 158453	Sabah	L	MK876515			MK876622	
D. trichocarpus	Anderson	20974	Sarawak	L.2182719	MK876517	MK876673	MK876569	MK876623	
Jatropha gossypiifolia	Snellius	11150	Lesser Sunda Islands	L.2236164	MK876567	MK876717	MK876613	MK876669	
Ostodes paniculata	Yu	172	Java	L	MK876520	MK876675	MK876571	MK876625	
Trigonostemon adenocalyx	Huang	H 09427	Guangxi, China	IBK 00214246	MK876547	MK876699	MK876594	MK876651	
T. albiflorus	Gillespie	7405	Vietnam	L.2260160	MK876527	MK876682	MK876578	MK876632	
T. aurantiacus	Yu	160	Java*	L	MK876529	MK876683	MK876579	MK876634	
T. balgooyi	Hisham	FRI 73820	Malay Peninsula	KEP 217032	MK876530	MK876684	MK876580	MK876635	
T. beccarii	Yu	169	Java*	L	MK876531	MK876685	MK876581	MK876636	
T. bonianus	Huang	NG 293	Guangxi, China	IBK 00214243	MK876541	MK876694	MK876590	MK876646	
T. capillipes	Gardner	ST 2836	Thailand	L.2260155	MK876535	MK876689	MK876585	MK876640	
T. cherrieri	Veillon	7420	New Caledonia	L.2260157	MK876536	MK876690	MK876586	MK876641	
T. detritiferus	Yu	91	Brunei	L	MK876538	MK876692	MK876588	MK876643	

Table 3 (cont.)

Taxa	Collector	Field No.	Location	Barcode	ITS	*trnK* intron	*trnT-L*	*trnL-F*	*rbcL*
T. diffusus	Pureseglove	P 4702	Sarawak	L.2260164	MK876539			MK876644	
T. filiformis	Yu	243	Philippines	L	MK876522	MK876677	MK876573	MK876627	MK876719
T. sp. aff. *filiformis*	Yu	SAN 158462	Sabah	L	MK876561	MK876711	MK876607	MK876663	
T. flavidus	Yu	264	Guangdong, China*	L	MK876540	MK876693	MK876589	MK876645	
T. hartleyi	Hartley	TGH 11087	New Guinea	L 0043309	MK876542	MK876695		MK876647	
T. inopinatus	Forster	PIF 30012	Australia	L.2260532	MK876543	MK876696	MK876591	MK876648	MK876723
T. laevigatus var. *laevigatus*	Yu	SAN 158478	Sabah	L	MK876544	MK876697	MK876592	MK876649	
T. lii	Huang	NG 306	Guangxi, China	IBK 00214245	MK876533	MK876687	MK876583	MK876638	
T. longifolius	Yu	SAN 158474	Brunei	L	MK876545	MK876698	MK876593	MK876650	
T. longipes	Yu	227	Philippines	L	MK876521	MK876676	MK876572	MK876626	MK876718
T. lychnos	Ali Ahmad	BRUN 19908	Brunei	SING 0179065	MK876546				
T. magnificus	de Wilde	19441	Sumatra	L.2260380	MK876548	MK876700	MK876595	MK876652	
T. malaccanus	Yu	176	Malay Peninsula	L	MK876549	MK876701	MK876596	MK876653	
T. merrillii	Yu	255	Philippines	L	MK876524	MK876679	MK876575	MK876629	MK876721
T. murtonii	Webb	WA 207	Cambodia	L.2260393	MK876551	MK876703	MK876598	MK876655	
T. pentandrus	Yu	FRI 86653	Malay Peninsula	L	MK876552	MK876704	MK876599	MK876656	
T. philippinensis	Bouman	RWB 67	Yunnan, China*	XTBG	MK876553	MK876705	MK876600	MK876657	
T. polyanthus	Lagrimas	PNH 39433	Philippines	L.2258802	MK876554				
T. quocensis	Middleton	4046	Thailand	L.2258834	MK876555	MK876706	MK876601	MK876658	
T. reidioides	Cheng	CL 1238	Cambodia	L.3784729	MK876556	MK876707	MK876602	MK876659	
T. rufescens	Yu	FRI 86664	Malay Peninsula	L	MK876557	MK876708	MK876603	MK876660	
T. sandakanensis	Yu	SAN 158473	Sabah	L	MK876559	MK876710	MK876605	MK876662	
T. semperflorens	Koelz	27866	India	L.2258764	MK876560		MK876606		
T. sp. 1	Yu	260	Philippines	L	MK876526	MK876681	MK876577	MK876631	

Table 3 (cont.)

Taxa	Collector	Field No.	Location	Barcode	ITS	*trnK* intron	*trnT-L*	*trnL-F*	*rbcL*
T. sp. 2	Koelz	27903	India	L.2260526	MK876532	MK876686	MK876582	MK876637	
T. sp. 3	Leong-Skornickova	OS 6243	Laos	SING 0190181	MK876528			MK876633	
T. verticillatus var. *salicifolius*	Worthington	13073	Malay Peninsula	L.2258554	MK876558	MK876709	MK876604	MK876661	
T. verticillatus var. *verticillatus*	Hai	HN-NY 503	Vietnam	L	MK876562	MK876712	MK876608	MK876664	
T. verrucosus	Chase	1274	Java*	K	MK883479	MK883481	MK883480	AY794703	
T. victoriae	Yu	258	Philippines	L	MK876525	MK876680	MK876576	MK876630	MK876722
T. villosus var. *borneensis*	Yu	SAN 158461	Sabah	L	MK876534	MK876688	MK876584	MK876639	
T. villosus var. *cordatus*	Yu	SAN 158479	Sabah	L	MK876537	MK876691	MK876587	MK876642	
T. villosus var. *merrillianus*	Yu	254	Philippines	L	MK876523	MK876678	MK876574	MK876628	MK876720
T. villosus var. aff. *merrillianus*	Yu	107	Brunei	L	MK876550	MK876702	MK876597	MK876654	
T. villosus var. *villosus*	Yu	178	Malay Peninsula	L	MK876564	MK876714	MK876610	MK876666	
T. viridissimus var. *viridissimus*	Julius	FRI 56285	Malay Peninsula	L.3795794	MK876563	MK876713	MK876609	MK876665	
T. wui	Yu	266	Guangdong, China*	L	MK876565	MK876715	MK876611	MK876667	
T. xyphophylloides	Yu	265	Guangdong, China*	L	MK876566	MK876716	MK876612	MK876668	
Tritaxis gaudichaudii	Soejarto	DDS 14143	Vietnam	L.3784654	MK876518	MK876674	MK876570	MK876624	

Table 4 Molecular primers used in the study. For ITS, the primers ITS5 + ITS4 were used to amplify the whole sequence, and two pairs of primers were designed for degraded or fungus-contaminated templates: for ITS1, ITS66F + ITS408R and for ITS2, ITS386F + ITS749R. For the *trnK* intron, the primers trnK 570F + 190R were used for the amplification. For *trnT-L* and *trnL-F*, the primers a + b and c + f were used to amplify the two sequences respectively, and two pairs of primers c + d and e + f were used for degraded templates to amplify the *trnL* intron and *trnL-F* spacer separately. In addition, two extra primers were designed to use together with c and f for greatly degraded templates to amplify the *trnL* intron in two pieces: c + t262R and t191F + d. For *rbcL*, the primers 1F + 724R and 636F + 1368R were used to amplify the gene in two parts.

Primer	Sequence	DNA marker	Reference
ITS5	5'-GGA AGT AAA AGT CGT AAC AAG G-3'	ITS	White et al. 1990
ITS4	5'-TCC TCC GCT TAT TGA TAT GC-3'	ITS	White et al. 1990
ITS66F	5'-CGA CCA GCG AAC ATG TTA TTC-3'	ITS	self-designed
ITS408R	5'-GGG ATT CTG CAA TTC ACA CCA AG-3'	ITS	self-designed
ITS386F	5'-CTT GGT GTG AAT TGC AGA ATC CC-3'	ITS	self-designed
ITS749R	5'-TTA AAC TCA GCG GGT GTT CCC-3'	ITS	self-designed
trnK570F	5'-TCC AAA ATC AAA AGA GCG ATT GG-3'	*trnK* intron	Samuel et al. 2005
190R	5'-CGA TCT ATT CAT TCA ATA TTT C-3'	*trnK* intron	Samuel et al. 2005
a	5'-CAT TAC AAA TGC GAT GCT CT-3'	*trnT-L*	Taberlet et al. 1991
b	5'-TCT ACC GAT TTC GCC ATA TC-3'	*trnT-L*	Taberlet et al. 1991
c	5'-CGA AAT CGG TAG ACG CTA CG-3'	*trnL-F*	Taberlet et al. 1991
d	5'-GGG GAT AGA GGG ACT TGA AC-3'	*trnL-F*	Taberlet et al. 1991
e	5'-GGT TCA AGT CCC TCT ATC CC-3'	*trnL-F*	Taberlet et al. 1991
f	5'-ATT TGA ACT GGT GAC ACG AG-3'	*trnL-F*	Taberlet et al. 1991
t262R	5'-CCT TTA CTT TAT CCT TTC TGG AG-3'	*trnL-F*	self-designed
t191F	5'-GGA GTT GAC TGC GTT GCA TTA G-3'	*trnL-F*	self-designed
1F	5'-ATG TCA CCA CAA ACA GAA AC-3'	*rbcL*	Lledo et al. 1998
636F	5'-GCG TTG GAG AGA TCG TTT CT-3'	*rbcL*	Lledo et al. 1998
724R	5'-TCG CAT GTA CCT GCA GTA GC-3'	*rbcL*	Lledo et al. 1998
1368R	5'-CTT CCA AAT TTC ACA AGC AGC A-3'	*rbcL*	Lledo et al. 1998

Table 5 Summary of sequence and alignment properties. The data of *trnL-F* and *rbcL* presented here only include the sequences obtained from this study. Matrix 1 includes sequences of all 5 markers obtained from this study aligned with the dataset of Euphorbiaceae based on *trnL-F* and *rbcL* sequences (Wurdack et al. 2005); matrix 2 includes the sequences of four markers obtained from this study: ITS, *trnK* intron, *trnT-L* and *trnL-F* . Note: the number before the slash (/) refers to matrix 1 and after the slash (/) to matrix 2.

DNA marker	No. taxa	Sequence length	Alignment length	Polymorphic sites	Variable sites	Parsimonious informative sites
ITS	61	282–754	693	0–25	311	169
trnK intron	49	335–498	570	0–1	98	31
trnT-L	47	323–528	640	0–1	99	30
trnL-F	57	372–1070	2327/1310	0–4	1310/196	888/55
rbcL	8	1390	1428	0–1	504	371
matrix 1	291	—	5658	—	2322	1489
matrix 2	62	—	3213	—	704	285

No significant indels (longer than 20 bp) are found in the major groups. The *trnK* intron alignment has 570 sites, including 98 variable and 31 parsimonious informative sites. A parsimony informative insertion of 25–40 bp is found at c. 195 bp upstream of the *matK* gene in 5 taxa (*Dimorphocalyx beddomei* (Benth.) Airy Shaw, *D. denticulatus* Merr., *Trigonostemon albiflorus* Airy Shaw, *T. wui* H.S.Kiu and *Tritaxis gaudichaudii*). The *trnT-L* alignment has 640 sites, of which 99 are variable and 30 are parsimonious informative. A parsimony informative insertion of 19 bp is found at c. 140 bp downstream of the *trnT* gene in *Trigonostemon longifolius* Wall. ex Baill. and *T. sandakanensis* Jabl. The alignment of the *trnL-F* sequences obtained from this study (part of matrix 2) contains 1310 sites, including 196 variable and 55 parsimony informative sites. A major parsimonious informative deletion of c. 29 bp is found in the *trnL* gene intron in 15 *Trigonostemon* taxa (*T. detritiferus* R.I.Milne, *T. diffusus* Merr., *T. filiformis* Quisumb., *T. flavidus* Gagnep., *T. longipes* (Merr.) Merr., *T. malaccanus* Müll.Arg., *T. murtonii* Craib, *Trigonostemon* sp. 1, *T. verticillatus* (Jack) Pax, *T. victoriae* R.Y.Yu & Welzen and some varieties of *T. villosus* Hook.f.). Also, an insertion of c. 62 bp was found in the *trnL-F* spacer of the outgroup (*Jatropha gossypiifolia* L.). When the *trnL-F* sequences are further aligned with Wurdack et al.'s (2005) dataset, the matrix (part of matrix 1) includes 2327 sites with 1310 variable sites and 888 of them are parsimony informative. In addition, *rbcL* sequences of seven *Trigonostemon* taxa were also aligned with the data of Wurdack et al. (2005). The *rbcL* matrix has 1428 sites, of which 504 are variable and 371 are parsimony informative. However, the eight *Trigonostemon* taxa (seven from our lab and *T. verrucosus* J.J.Sm. from Wurdack et al. 2005) in this matrix display very little variation, with only 34 variable and 11 parsimony informative sites and no indels.

A significant number of polymorphisms are found in the ITS sequences, particularly in *Trigonostemon albiflorus* (25 sites) and *Dimorphocalyx* sp. (15 sites). For other markers, polymorphic sites are always fewer than 4 per taxon.

Analyses of the combined dataset (***matrix 1***)

The MP and BI analyses result in the same topology (Figure 41) for the main clades as Wurdack et al. (2005), although the bootstrap supports and posterior probabilities of some clades are relatively lower. This is probably because of the large amount of absent data in the taxa obtained from Wurdack et al. (2005), because they did not analyse the nuclear ITS and chloroplast *trnK* intron and *trnT-L* sequences.

The species of *Trigonostemon* form a monophyletic group in the C2 clade (99 MP bootstrap credibility and 1.0 posterior probability; Figure 41); so do the *Dimorphocalyx* species (including *Tritaxis gaudichaudii*, discussed below), but the group has relatively lower support (66 MP bootstrap credibility and 0.89 posterior probability). *Ostodes paniculata* Blume (two samples) appears to be sister to *Vernicia montana* Lour. with a posterior probability of 0.72 (Figure 41). The relationships between *Trigonostemon*, *Dimorphocalyx* and *Ostodes* are still unresolved.

Analyses of Trigonostemon and its close relatives only (***matrix 2***)

In general, the ITS yields more variation than the chloroplast markers (*trnK* intron, *trnT-L* and *trnL-F*), but the phylograms (Figures 43–46) obtained separately from the nuclear and chloroplast markers have similar topologies for the main clades. In both phylograms *Trigonostemon* forms a monophyletic group and includes three main clades (less resolved in the chloroplast phylogram). However, in the BI phylogram (Figure 45) based only on the chloroplast markers, *Dimorphocalyx malayanus* Hook.f. is oddly placed as a sister taxon of

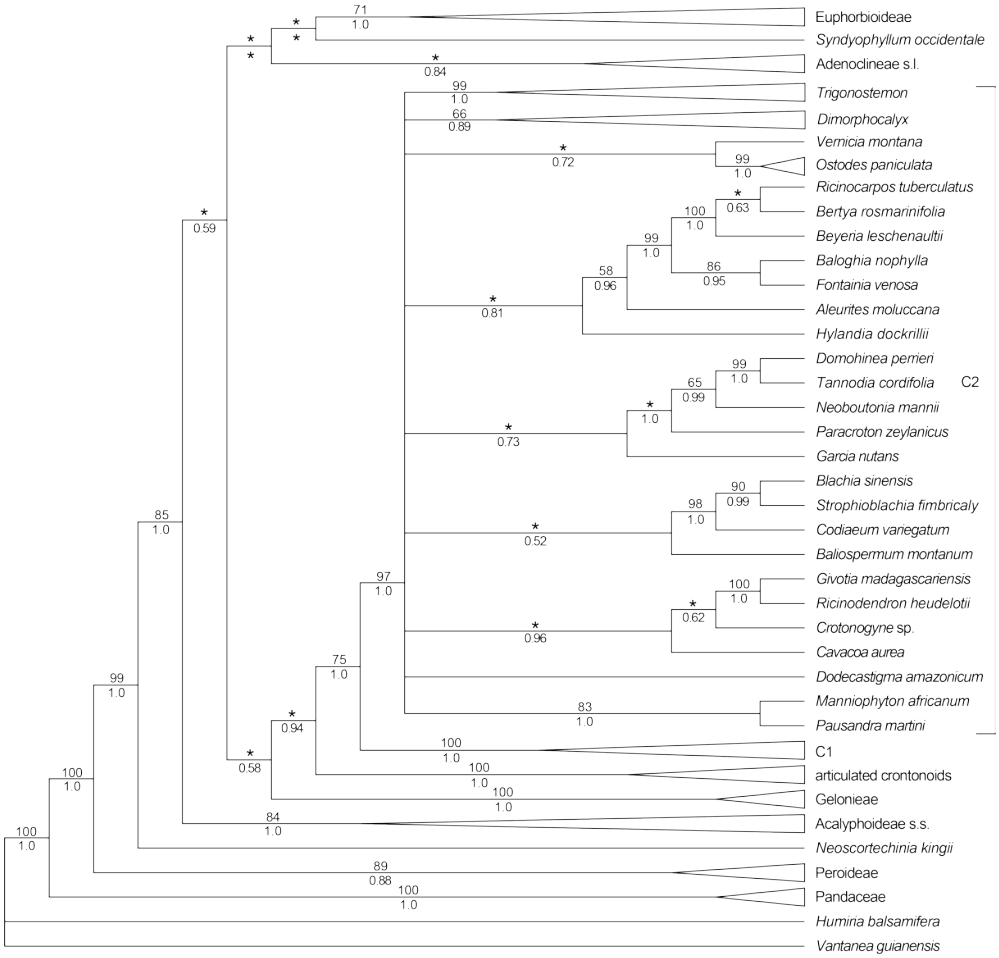

Figure 41 Phylogenetic position of *Trigonostemon*, *Dimorphocalyx* (now *Tritaxis*) and *Ostodes* in the Euphorbiaceae, resulting from the Maximum Parsimony and Bayesian Inference analyses of combined nuclear ITS and chloroplast *trnK* intron, *trnT-L*, *trnL-F* and *rbcL* data obtained from this study and Wurdack et al. (2005). The number above the clades is the bootstrap credibility from the MP analysis, and the number below the clades is the posterior probability from the BI analysis. Clades are omitted when the bootstrap support is below 50 or the posterior probability is below 0.5, except where marked with an asterisk. The figure is a summary of Wurdack et al. (2005) and the triangles represent groups of species (or specimens in the case of *Ostodes*).

Ostodes, but this is likely because the chloroplast data of *D. malayanus* is largely missing (only part of the *trnL-F* sequence was included; see Table 3); *Dimorphocalyx australiensis* C.T.White forms a polytomy with all other clades because of a low posterior probability (but still within the *Dimorphocalyx* clade in the maximum clade credibility tree). The four markers are combined as one dataset for analyses and for the discussion below.

The trees made by the three methods (MP, ML and BI) have the same topology for the main clades in the majority rule consensus trees (Figures 42, 47, 48), except in the MP analysis, *Ostodes paniculata* is branching outside *Dimorphocalyx* and *Trigonostemon* (Figure 47). This discrepancy, however, does not change the monophyly of the *Dimorphocalyx* and *Trigonostemon* clades.

The MP analysis resulted in a total of 732,240 trees as the best score. In the 50% majority-rule consensus tree, the frequency of occurrence is always 100, except in some minor clades within the T1 group. Two major parsimony informative indels appear to support the phylogeny (Figure 47): 1. the insertion in the *trnT* gene of *Trigonostemon longifolius* and *T*. *sandakanensis*; 2. the deletion in the *trnL-F* spacer of several *Trigonostemon* taxa in the T1 clade. The insertion in the *matK* gene in 5 taxa (*Dimorphocalyx beddomei*, *D*. *denticulatus*, *Trigonostemon albiflorus*, *T*. *wui* and *Tritaxis gaudichaudii*) does not support the phylogeny.

A noteworthy discrepancy in the results among the different methods is in the placement of three *Trigonostemon* species collected from China (*T*. *adenocalyx* Gagnep., *T*. *bonianus* Gagnep. and *T*. *lii* Y.T.Chang): they always cluster as one group with strong support in all analyses (100 both MP and ML credibility, 1.0 posterior probability), but in the MP and ML analyses this group is branching at the base of the T3 clade (71 both MP and ML bootstrap credibilities for the ingroup of T3, Figures 47, 48), whereas in the BI analysis, it is one node higher inside the T3 clade, leaving four species, *T*. *aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl., *T*. *hartleyi* Airy Shaw, *T*. *philippinensis* Stapf and *T*. *xyphophylloides* (Croizat) L.K.Dai & T.L.Wu branching at the base of the T3 group (1.0 posterior probability for the ingroup, Figure 42).

In the phylogram (Figure 42), *Trigonostemon* and *Dimorphocalyx* form their own monophyletic groups with strong support (100 both MP and ML bootstrap credibility, 1.0 posterior probability for *Trigonostemon*; 96 both MP and 97 ML bootstrap credibility, 0.99 posterior probability for *Dimorphocalyx*). *Tritaxis gaudichaudii* is embedded in the *Dimorphocalyx* clade, therefore, the two genera are merged together in the taxonomic treatment (discussed below). *Ostodes* (only one taxon sampled) does not fit in either *Trigonostemon* or *Dimorphocalyx* and is regarded as a separate genus.

Within *Trigonostemon*, three well supported major clades (T1, T2, T3) can be recognised, of which the T1 and T2 clades are sister clades. Several morphological and pollen characters are also mapped on the phylogram (Figure 42).

DISCUSSION

Generic delimitations of Trigonostemon, Dimorphocalyx and Ostodes

Only one taxon of *Trigonostemon* (*T*. *verrucosus*) was included in the phylogenetic analyses of the uniovulate Euphorbiaceae by Wurdack et al. (2005). The taxon was branching in the C2 clade of the Crotonoideae. Our results (Figures 41, 42), with 47 more taxa of *Trigonostemon*, confirm its phylogenetic position, and clearly show monophyly of the genus.

Dimorphocalyx (c. 13 species mainly occur in SE Asia, van Welzen & van Oostrum 2015) was established based on *D*. *glabellus* Thwaites (1861), a species with two whorls of stamens (5+5) of which only the inner whorl has connate stamens. The genus is also monophyletic and is separate from *Trigonostemon* in both molecular analyses (Figures 41, 42). The precise relationship between *Dimorphocalyx* and *Trigonostemon* is still unclear (Figure 41), as the relationships of most genera in the C2 clade are still unresolved. Moreover, *Dimorphocalyx* can be morphologically distinguished from *Trigonostemon* by its predominantly dioecious sexual system (vs. always monoecious in the latter), the stamens being more than 7 and often arranged in two (or three) whorls (Figure 40k; vs. 3 or 5 connate stamens in a single whorl in *Trigonostemon*, Figure 40a–d), and the white petals (Figure 40k; vs. petals of various colours including white in *Trigonostemon*, Figure 40a, b, e, f). Therefore, following most botanists

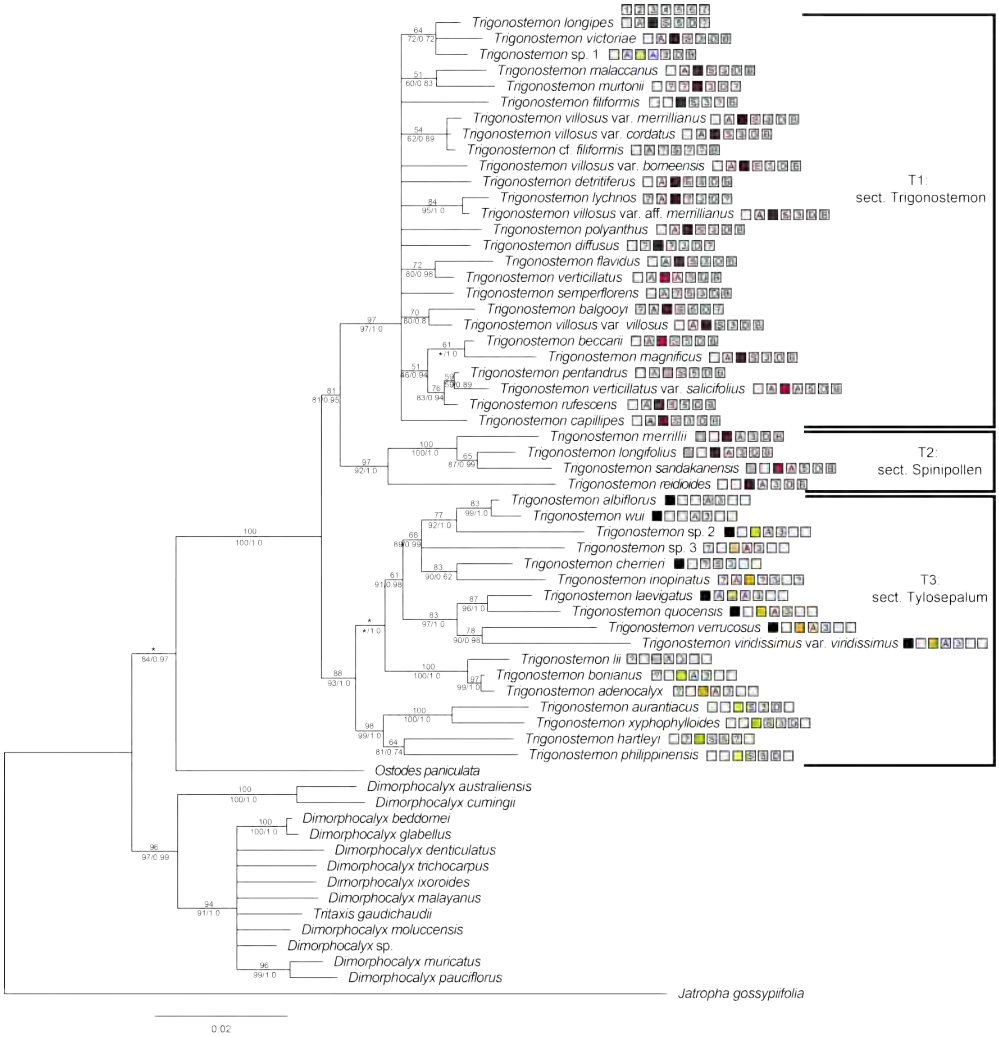

Figure 42 Phylogenetic relationship of selected species of *Trigonostemon*, *Dimorphocalyx* (now *Tritaxis*), *Ostodes* and *Tritaxis gaudichaudii* based on nuclear ITS and chloroplast *trnK* intron, *trnT-L* and *trnL-F* sequences. The branch lengths are based on the BI method. The number above the clades is the bootstrap credibility from the MP analysis, and the numbers below the clades are the bootstrap credibility from the ML analysis and the posterior probability from the BI analysis. The clades are omitted if the MP or ML bootstrap credibility is below 50. Asterisks indicate a different topology of the relevant clade in the MP or ML analysis. Next to each taxon of *Trigonostemon* are seven characters of the pollen and macromorphology (from left to right): 1. pollen type: ☐ = *Trigonostemon reidioides* type and subtype pollen, ▩ = *Trigonostemon reidioides* type *Trigonostemon longifolius* subtype pollen, ■ = *Trigonostemon verrucosus* type pollen; 2. pistillate sepals: A = accrescent when fruiting, ☐ = not accrescent; 3. the colour of petals; 4. disc shape (both sexes): S = scales, A = annular; 5. number of stamens; 6. anthers: D = divaricate at the top, ☐ = not divaricate; 7. stigmas: B = deeply bifid, ☐ = not obviously bifid; ? = unknown.

(e.g., Bentham 1878, 1880 and Pax 1890), we keep *Trigonostemon* and *Dimorphocalyx* as two separate genera.

Tritaxis was described in 1858 by Baillon, three years earlier than *Dimorphocalyx*, mainly on the basis of the three whorls of stamens in the type species, *T. gaudichaudii* Baill. (hence its name; for illustration see Gagnepain 1925b). In the following years, a few more species were published under *Tritaxis*, but they were then all transferred to other genera (see Introduction and Taxonomic treatment). The type species of *Tritaxis*, *T. gaudichaudii*, is embedded in the *Dimorphocalyx* clade (Figure 42), indicating the congeneric status of the two genera. Furthermore, by the modern generic definition of *Dimorphocalyx*, species with three whorls of stamens are included in the genus (van Welzen & van Oostrum 2015), which also lends weight to merging these two genera together. Because *Tritaxis* is an older name, *Dimorphocalyx* is now treated as its synonym.

The rare species *Dimorphocalyx cumingii* (Müll.Arg.) Airy Shaw, endemic to the Philippines, was originally proposed under *Trigonostemon* sect. *Anisotaxis*, but was later treated under *Tritaxis* (Bentham 1878; Pax 1910; Merrill 1923) or *Dimorphocalyx* (Airy Shaw 1969), because different delimitations of *Trigonostemon* were applied. The species has fewer stamens (8–9, in two whorls) and more condensed inflorescences than most *Dimorphocalyx* species, but the characters are still well in line with *Dimorphocalyx*. This is also supported by the molecular phylogeny, as it is embedded in the *Dimorphocalyx* clade (Figure 42) sister to *D. australiensis* C.T.White. As a result of the synonymisation discussed above, the name *Tritaxis cumingii* (Müll.Arg.) Benth. is the accepted name.

Ostodes is a small genus with two species characterised by a relatively bigger tree size (up to 16 m tall and a diameter at breast height up to 40 cm) and more stamens (20–41, Figure 40l) compared to *Dimorphocalyx* and *Trigonostemon*. The pistillate calyx does not enlarge when mature, which is also obviously different from the other two genera. In the molecular analyses (Figure 41), *Ostodes* is separate from both *Dimorphocalyx* and *Trigonostemon* as a unique clade, potentially sister to *Vernicia montana* (0.77 posterior probability). *Vernicia* Lour. is also a small genus with three morphologically similar species (Stuppy et al. 1999, 2005). The genus is quite different from *Ostodes*, as *Vernicia* often has lobed leaves with different basilaminar glands (also in the sinuses when lobed), much larger flowers, different disc glands in both sexes, the stamens are much more united (also the outer whorl) than *Ostodes*, and the fruits are much larger, tardily dehiscent and up to 5-locular. *Vernicia* was not included in our matrix 2 and the phylogeny by Wurdack et al. (2005) does not show enough resolution, thus more molecular analyses are needed to solve the relationships. As both genera are easy to separate and recognize, we refrain from uniting them.

Evolution of the 'croton pattern' ornamentation in pollen morphology

Within the *Trigonostemon* group, three major clades can be recognised, noted as T1, T2 and T3 (Figure 42). These clades correlate well with the pollen morphology of the genus (Yu et al. 2019c; Figure 42 character 1). Generally, the species in clade T1 have *Trigonostemon reidioides* type and *reidioides* subtype pollen (Figure 40m, n), whereas the T2 clade represents the *Trigonostemon reidioides* type *longifolius* subtype pollen (Figure 40o, p) and the T3 clade the *Trigonostemon verrucosus* type pollen (Figure 40q, r).

It is noteworthy that the taxa that basally branch in the T2 and T3 clades, i.e., *T. reidioides* (T2), and *T. aurantiacus*, *T. hartleyi*, *T. philippinensis* and *T. xyphophylloides* (T3), also have

the same pollen as the T1 clade, while their sister groups are both monophyletic with good supporting values (97 MP and 92 ML bootstrap credibility and 1.0 BI posterior probability in the T2 clade, 88 MP and 93 ML bootstrap credibility and 1.0 BI posterior probability in the T3 clade). Moreover, the *reidioides* subtype pollen bears the same tectum ornamentation as in the outgroups *Dimorphocalyx*, *Ostodes* and *Jatropha*; thus the 'croton pattern' ornamentation with clearly discernible obtuse 'subunits' is plesiomorphic, except that the pollen is considerably smaller in the average size (Yu et al. 2019c). On the other hand, the *longifolius* subtype pollen and the *Trigonostemon verrucosus* type pollen are probably never found in any other taxa in the Euphorbiaceae. This potentially reveals an evolutionary trend in which the common 'croton pattern' ornamented pollen in the Euphorbiaceae starts specializing in *Trigonostemon* in two directions: in the T2 clade, the 'croton pattern' ornamentation remains but the subunits reduce to spines; in the T3 clade, the 'croton pattern' ornamentation collapses by merging the subunits together into bigger 'lumps' supported by more collumellae.

A difference in the position of three species in the T3 clade was found between the trees reconstructed by different methods (see Results), but the pollen morphology of these three species (*T. adenocalyx*, *T. bonianus* and *T. lii*) is unknown. Thus, they are not considered in the discussion here for the moment. Pollen of *Trigonostemon inopinatus* Airy Shaw (Figure 40s, t) appears aberrant among all the other species as it has lost the 'croton pattern' ornamentation but has many 'spines' on the muri of the tectum. It was temporarily classified in the *Trigonostemon reidioides* type *longifolius* subtype, but molecular phylogeny shows that it belongs to the T3 clade, together with species with the *Trigonostemon verrucosus* type pollen. This also conforms with our discussion of the loss of 'croton pattern' ornamentation in the T3 clade.

Infrageneric classification of Trigonostemon

Morphologically, species of the T3 clade are easiest to distinguish from the others, irrespective of the discrepancy in the placement of *T. adenocalyx* Gagnep., *T. bonianus* Gagnep. and *T. lii* Y.T.Chang (see above): they have lighter colours in petals, often white, yellow to orange (Figure 40b, f; Figure 42 character 3) compared to often dark reddish purple (Figure 40e) in the other two clades; the stigmas are not bifid or sometimes only with a very shallow groove at the top (Figure 40f, h; Figure 42 character 7), whereas in the other species, the stigmas are always deeply divided (Figure 40e, g). In addition, the sepals of pistillate flowers are often not much accrescent (for example of accrescent/non-accrescent sepals, see Figure 40i, j; Figure 42 character 2) except for *T. inopinatus*. Two sub-groups of the T3 clade are distinguished from each other by the stamens: divaricate at apex (for example of divaricate stamens, see Figure 40a, c; Figure 42 character 6) forming a V-shaped structure with an often conical appendix (see the description of *Prosartema* Gagnep. [= *Trigonostemon*], Gagnepain 1924b) or numerous cells of secretion on the connective (discussed in Yu & van Welzen 2018) in *T. aurantiacus*, *T. philippinensis* and *T. xyphophylloides* (unknown for *T. hartleyi*), which is also present in the T1 and T2 clades; in the other species, the anthers are short and round without splitting at the top (for example, see Figure 40b, d; stamens sometimes very slightly divaricate as in *T. capitellatus*).

The T1 and T2 clades have a closer relationship: these clades ally with each other as a sister of the T3 clade in the phylogram (supported by 81 both MP and ML bootstrap credibility and 0.95 BI posterior probability). This is reflected in their closer pollen ('croton pattern' ornamentation, see above) and macromorphology: often dark reddish purple petals (except for *Trigonostemon* sp. 1), divaricate stamens (for example, see Figure 40a, c) and bifid stigmas (for example, see

Figure 40e, g). However, they are different in the pistillate sepals and disc shape: in the T1 clade the pistillate sepals are often obviously accrescent when fruiting (they are at least twice the size as those in the staminate flowers; for example, see Figure 40j; Figure 42 character 2) and the disc comprises separate lobes or glands (except in *T*. *verticillatus*; for example, see Figure 40c, g; Figure 42 character 4), whereas in the T2 clade, the pistillate sepals are not much accrescent (for example, see Figure 40i) and the disc is annular (for example, see Figure 40d). Moreover, the division in the stigma in the T2 clade is often shallower than in the T1 clade.

The number of stamens (either 3 or 5) is considered an important character for species delimitation (Yu & van Welzen 2018), because it provides a reliable evidence of morphological discontinuity. However, this character does not strictly correspond to any of the clades (Figure 42 character 5), therefore, it is not used in the infrageneric classifications.

Among the previous infrageneric classifications, Jablonski's (1963) seems the closest to the molecular phylogeny, as he precisely recognised the importance of the division of the stigmas and the variation in stamens, but he wrongly designated *T*. *longifolius* as the type for sect. *Trigonostemon* (because the autonymous section has the same type as the genus, i.e., | *T*. *serratus*, even though the latter was not included in his revision), resulting in misplacements of species in sect. *Telogyne* Baill., which should be sect. *Trigonostemon*. Also, *T*. *laevigatus* Müll.Arg., according to his criteria, should be placed in sect. *Tylosepalum* (Kurz) Benth. not sect. *Trigonostemon*, but this was because of lack of material.

The molecular phylogeny suggests three sections for the genus. Although the type species of *Trigonostemon*, *T*. *serratus*, is not included in the molecular phylogeny (no suitable material available), its morphology, e.g., the accrescent pistillate sepals, glandular disc, divaricate stamens and bifid stigmas strongly indicates a position within the T1 clade, which therefore, forms the autonymous sect. *Trigonostemon*. A new sect. *Spinipollen* R.Y.Yu & Welzen is proposed for the T2 clade with *T*. *longifolius* as type, and the T3 clade represents a third sect. *Tylosepalum* with *T*. *aurantiacus* as type. In addition, Bentham (1878) proposed the sect. *Pycnanthera* Benth. for *T*. *diplopetalus* Thwaites and *T*. *nemoralis* Thwaites, which are two rare species characterised by the sessile stamens adnate to a greatly thickened connective (or joined connectives). These two species have a strictly limited distribution: *T*. *diplopetalus* is endemic to Sri Lanka and *T*. *nemoralis* is only distributed in Travancore (S India) and Sri Lanka. No material was available for the molecular analyses (for more descriptions and illustrations of the species, see Trimen 1898, Balakrishnan & Chakrabarty 1991 and Philcox 1997), but their greatly thickened connective, among others, certainly displays a morphological discontinuity and therefore sets them apart from other species as a separate sect. *Pycnanthera* (not included in the phylogeny; Figure 42). *Trigonostemon diplopetalus* is selected as the type of this section. There is one exception in the literature citations in the taxonomic treatment: Pax & Hoffmann (1911) also included *Trigonostemon lanceolatus* (S.Moore) Pax in sect. *Pycnanthera*, but based on its morphology it most likely belongs to sect. *Trigonostemon*.

Taxonomic treatment of *Trigonostemon*

The accepted species are based on Yu & van Welzen (2018), Balakrishnan & Chakrabarty (1991), Phattarahirankanok & Chayamarit (2005) and Li & Gilbert (2008); only the protologue of each taxon is given.

Trigonostemon Blume, Bijdr. Fl. Ned. Ind. (1825) 600 ('*Trigostemon*'); Fl. Javae (1828) Preface 8 (name corrected in note), nom. et orth. cons. — Type: *Trigonostemon serratus* Blume.
Enchidium Jack, Malayan Misc. 2 (1822) 89, nom. rej. — Type: *Enchidium verticillatum* Jack [= *Trigonostemon verticillatus* (Jack) Pax].

Key to the sections

1. Stigmas deeply bifid (at least 1/2 the length of stigma) 2
1. Stigmas not or slightly (less than 1/2 the length of stigma) divided (often bifid; but twice divided in *T. diplopetalus*) 3
2. Pistillate sepals accrescent when fruiting (at least twice the size as those in staminate flowers), disc (both staminate and pistillate flowers) of five scales or glands (except annular with 5-toothed protrusions in *T. verticillatus*)..... sect. 1. ***Trigonostemon***
2. Pistillate sepals not accrescent when fruiting, disc (both staminate and pistillate flowers) annular ..... sect. 2. ***Spinipollen***
3. Petals white, yellow, orange, occasionally light pinkish red; filamens connate as an androphore.....sect. 3. ***Tylosepalum***
3. Petals red or dull purple; filaments absent, anthers sessile, clustered on a greatly thickened connective (or joined connectives).....sect. 4. ***Pycnanthera***

1. ***Trigonostemon*** sect. ***Trigonostemon*** — Type: *Trigonostemon serratus* Blume.

Silvaea Hook. & Arn., Bot. Beechey Voy. (1837) 211. — *Trigonostemon* Blume sect. *Silvaea* (Hook. & Arn.) Müll.Arg., Linnaea 34 (1865) 214. — Type: *Silvaea semperflorens* (Roxb.) Hook. & Arn. [= *Trigonostemon semperflorens* (Roxb.) Müll.Arg.].
Telogyne Baill., Étude Euphorb. (1858) 327, pl. 11, f. 13. — *Trigonostemon* Blume sect. *Telogyne* (Baill.) Müll.Arg., Linnaea 34 (1865) 214. — Type: *Telogyne indica* Baill. [= *Trigonostemon verticillatus* (Jack) Pax].

1. ***Trigonostemon balgooyi*** R.Y.Yu & Welzen, Blumea 62 (2018) 188, f. 2. — Type: *van Balgooy 7102* (holo L, barcode L.2258686; iso K, KEP, barcode KEP222394, L, barcode L.2258685, SAN, accession 051745), Malaysia, Johor, Endau-Rompin, Kuala Jasin, 2°32'N, 103°22'E, 100 m, lowland rainforest on clay soil, 1 Mar 1996.

2. ***Trigonostemon beccarii*** Ridl., Bull. Misc. Inform. Kew (1925) 89. — Type: *Beccari PS 965* (BM, K, barcode K000959300, L, barcode L0016478), Indonesia, Sumatra, Padang, Sungei Buluh, Sep 1878.

3. ***Trigonostemon capillipes*** (Hook.f.) Airy Shaw, Kew Bull. 20 (1967) 413. — Type: *Lobb s.n*. (K, barcode K000894763), Singapore.

4. ***Trigonostemon detritiferus*** R.I.Milne, Kew Bull. 49 (1994) 446, f. 2. — Type: *Dransfield 6913* (holo K, barcode K000959297; iso BRUN, accession B008840, K, barcode K000959298), Brunei, Temburong, Selapon, village margin, 4°40'N, 115°12'E, 15 m, old secondary forest on alluvial flat, 18 Nov 1990.

5. ***Trigonostemon diffusus*** Merr., Sarawak Mus. J. 3 (1928) 525. — Type: *Mjöberg 145* (BM, K, barcode K000959296, UC, barcode UC231637), Malaysia, Sarawak, foot of Mt. Poi, 1924.

6. ***Trigonostemon filiformis*** Quisumb., Philipp. J. Sci. 41 (1930) 328, f. 7. 1930. — Type: *Clemens 16751* (A, barcode A00048894, NY, barcode NY00273349, UC, barcode UC347527), Philippines, Luzon, Isabela, Mt. Moises, Apr 1926.

7. ***Trigonostemon flavidus*** Gagnep., Bull. Soc. Bot. France 69 (1922) 749. — Type: *Harmand 3273* (P, barcodes P00717104, P00717105), Laos, in Mount Lakhon near Me-Kong, Sep 1877.

8. ***Trigonostemon longipes*** (Merr.) Merr., Philipp. J. Sci. 11 (1916b) 191. — Lectotype (designated by Yu & van Welzen, 2018): *FB* (*Whitford*) *1066* (lecto K, barcode K000959374; isolecto P, barcode P00648673), Philippines, Luzon, Bataan, Mount Mariveles, Jan 1905.

9. ***Trigonostemon lychnos*** (R.I.Milne) R.Y.Yu & Welzen, Blumea 62 (2018) 201. — Type: *Coode 6766* (holo K, barcode K000959280; iso BRUN, accession B013567), Brunei, Belait, Andulau Forest Reserve, compartment 7, 4°35'N, 114°33'E, forest, 14 Apr 1990.

10. ***Trigonostemon magnificus*** R.I.Milne, Kew Bull. 50 (1995b) 51, f. 1, ('*magnificum*'). — Type: *de Wilde & de Wilde-Duyfjes 19441* (holo K, barcode K000959284; iso BO, accession BO1835092, BO, no accession number, K, barcode K000959283, KLU, accession J2349, L, barcode L.2260380, P, barcode P04804057), Indonesia, Sumatra, Aceh, c. 75 km WNW of Medan, Gunung Leuser National Park, Sikunder Forest Reserve, Besitang River, c. 3°55'N, 98°05'E, 50–100 m, marshy forest, 6 Aug 1979.

11. ***Trigonostemon malaccanus*** Müll.Arg., Flora 47 (1864a) 482. — Type: *Griffith KD 4782* (K, barcode K000959325), Malaysia, Malacca.

12. ***Trigonostemon murtonii*** Craib, Bull. Misc. Inform., Kew (1911) 464, ('*murtoni*'). — Type: *Murton 18* (K, barcode K000959311), Thailand, west coast, Koh Klone.

13. ***Trigonostemon pentandrus*** Pax & K.Hoffm. in Engl., Pflanzenr. IV.147 vii (1914) 406. — Neotype (designated by Yu & van Welzen, 2018): *KEP FRI* (*Yu*) *86653* (neo L; isoneo KEP), Malaysia, Negeri Sembilan, Gunung Angsi, Bukit Putus to Angsi summit, before the first rest gazebos, mixed forest, understorey on sandy soil, 16 Dec 2018.

14. ***Trigonostemon polyanthus*** Merr., Philipp. J. Sci. 9 (1914) 492. — Type: *BS* (*Ramos*) *1645* (BM, BO, accession BO1722340, BRI, barcode BRI-AQ0342683, CAL, barcode CAL0000023675, G, barcode G00435098, GH, barcode GH00048899, L, barcode L.2258801, NY, barcode NY00273354, P, barcode P00717156, SING), Philippines, Samar, Cauayan Valley, Apr 1914.

15. ***Trigonostemon rufescens*** Jabl., Brittonia 15 (1963) 152, f. 2. — Type: *SFN* (*Corner*) *29428* (holo SING, barcode SING0051354; iso A, barcode A00048887, BO, K, barcode K000959319, L, barcode L.2258748, SAN, accession 0106235), Malaysia, Johore, 13.5 miles on Mawai – Jemaluang Road, altitude low, 13 May 1935.

16. ***Trigonostemon semperflorens*** (Roxb.) Müll.Arg. in A.DC, Prodr. 15 (1866) 1110. — Lectotype (designated here): Roxburgh's *Flora Indica* drawing, no. 2401 (CAL).

17. ***Trigonostemon verticillatus*** (Jack) Pax in Engl., Planzenfam. IV.147 iii (1911) 87. — Neotype (designated by Yu & van Welzen, 2018): *Maingay 1403* (neo L, barcode L.2258683; isoneo BM, CAL, barcode CAL0000031928, K), Malaysia, Penang.

18. ***Trigonostemon victoriae*** R.Y.Yu & Welzen in Blumea 62 (2018) 215, f. 15. — Type: *PNH* (*Sulit*) *12317* (holo L, barcode L.2260416; iso L, barcode L.2260417, PNH, on 3 sheets), Philippines, Palawan Province, Aborlan, Panacan, SE base of Victoria Mountains, partially open at the bank of Karaniogan river, 10 May 1950.

19. ***Trigonostemon villosus*** Hook.f., Fl. Brit. India 5: 397. 1887. — Syntypes: *King's collector s.n*. (K, barcode K000959324), Malaysia, Perak; *King's collector 4819* (CAL, barcode CAL0000023668), Malaysia, Perak, Larut, Gopeng, 500–800 ft, Aug 1883; *King's collector 2400* (CAL, barcode CAL0000023669), Malaysia, Perak, Larut, 1000–2000 ft, Sep 1881.

The following species are not included in the molecular phylogeny but also belong to this section based on morphology:

20. ***Trigonostemon calcicolus*** (R.I.Milne) R.Y.Yu & Welzen, Blumea 62 (2018) 189. — Type: *Chew 679* (holo K, barcode K000959281), Malaysia, Sarawak, 1st Division, Kuching District, Tiang Bekap, Mt. Mentawa, 1°12' N, 110°23'E, 250 ft, on limestone.

21. ***Trigonostemon dipteranthus*** Airy Shaw, Kew Bull. 20 (1966) 47. — Type: *Korthals s.n*. ('*853*') (L, barcode L0160131), Sumatra, West Coast Res., Padang.

22. ***Trigonostemon kerrii*** Craib, Bull. Misc. Inform., Kew (1924) 97. — Lectotype (designated by Chantaranothai 2005): *Kerr 5871* (lecto BK, barcode BK239811; isolecto A, barcode A00048870, P, barcode P04810877), Thailand, Nakawn Tai, c. 200 m, evergreen forest, 17 Apr 1922.

23. ***Trigonostemon laetus*** Baill. [Étude Euphorb. (1858) 341, nom. nud.] ex Müll.Arg. in A.DC., Prodr. 15 (1866) 1109. — Type: *Wallich 7740B* (syn G-DC, barcodes G00319757, on 2 sheets, G00319769, P, barcodes P00717111, P00717112; isosyn: CAL, barcode CAL0000023673), Myanmar, Amherst.

24. ***Trigonostemon lanceolatus*** (S.Moore) Pax in Engl., Pflanzenr. IV.147 iii (1911) 93. — Type: *Beddome s.n*. (BM, barcode BM000951502), Myanmar, Tenasserim, Mooleyit slopes.

25. ***Trigonostemon pierrei*** Gagnep., Bull. Soc. Bot. France 69 (1922) 752. — Type: *Pierre 1530* (A, barcode A00048875, K, barcode K000959307, P, barcodes P00717121, P00717122, P00717123, US, barcode US00096541), Vietnam, in insula Phu Quoc ad montibus Ong Chao, Apr 1874.

26. ***Trigonostemon phyllocalyx*** Gagnep, Bull. Soc. Bot. France 69 (1922) 753. — Type: *Poilane 2700* (A, barcode A00048879, P, barcodes P00717119, P00717120), Vietnam, Annam, Nhatrang, versant grande montagne de Dông-Bô, versant de la mer NE, 5 Mar 1922.

27. ***Trigonostemon scopulatus*** R.Y.Yu & Welzen, Blumea 62 (2018) 210, f. 14. — Type: *KEP FRI* (*Cockburn*) *7859* (holo L, barcode L.2258747; iso K, KEP, barcode KEP157633, SING, accession 531533), Malaysia, Johore, Ulu Endau, Labis FR, compartment 277, disturbed forest near logging road, 22 Mar 1968.

28. ***Trigonostemon serratus*** Blume, Bijdr. Fl. Ned. Ind. (1825) 600, ('*serratum*'). — Lectotype (designated by Yu & van Welzen, 2018): *Blume 1648* (lecto L, barcode L.2258717; isolecto L, barcodes L.2258713, L.2258714, L.2258716), Indonesia, Java.

29. ***Trigonostemon sinclairii*** Jabl., Brittonia 15 (1963) 154, f. 3, 4. — Type: *SFN* (*Sinclair & Kiah bin Salleh*) *40418* (holo SING), Malaysia, Terengganu, Block 3B, Gunong Tebu F.R., 51st mile Kuala Terengganu – Berut Road, 10 Nov 1954.

30. ***Trigonostemon wetriifolius*** Airy Shaw & Ng, Malaysian Forester 41 (1978) 237, f. 1–3. — Type: *KEP FRI* (*F.S.P. Ng*) *27157* (holo K; iso KEP), Malaysia, S Pahang, Lesong Forest Reserve in proposed Endau-Rompin National Park, primary forest under logging, 6 Sep 1977.

31. ***Trigonostemon wildeorum*** R.Y.Yu & Welzen, Blumea 62 (2018) 222, f. 20. — Type: *de Wilde & de Wilde-Duyfjes 20274* (holo L, barcode L.2258570; iso L, barcode L.2258569, BO, accessions BO000954, BO000955), Indonesia, Sumatra, Aceh, Middle Alas River (Lae Sauraya) area, c. 15 km N of Gelombang, S of Bengkong River, 2°55' N, 99°57'E., c. 50 m, foot hill forest, on yellow-red loamy soil, 23 Jul 1985.

2. ***Trigonostemon*** sect. ***Spinipollen*** R.Y.Yu & Welzen, *sect. nov.* — Type: *Trigonostemon longifolius* Wall. ex Baill.

Diagnosis: Pistillate sepals not accrescent; petals in both staminate and pistillate flowers spathulate, base claw-like, disc annular; stigmas apically bifid into 2 arms.

Description: Shrubs or small trees. *Stipules* subulate to falcate, often pubescent. *Leaves*: petiole up to 3.5 cm long, often less than 1/7 the length of the blade, hairy; blade oblanceolate, oblong to elliptic, 4–46 by 1–15 cm, glabrous or hairy. *Inflorescences* unisexual or bisexual, axillary or terminal, paniculate or thyrsoid, flowers arranged in racemes or clustered in very short cymes or glomerules along the main rachis. *Staminate flowers*: pedicel slender, pubescent, base articulate; sepals elliptic, margin entire or undulate, apex acute to rounded, glabrous or pubescent outside, glabrous inside; petals often spathulate, pink, red, dark purple or rarely white, base slightly claw-like, outer surface glabrous, inner surface glabrous or very rough (*T. sandakanensis*), sometimes with 2 gland lobes (*T. longifolius*); disc annular; stamens 3 or 5, connate in a column, anthers divaricate, connective often apically forming an appendage with few expanded cells of secretion; pollen grains with 'croton pattern' ornamentation, subunits reduced to spines. *Pistillate flowers*: pedicel longer and broader than staminate ones; sepals very slightly or not accrescent when fruiting; petals and disc as staminate flowers; ovary slightly to densely pubescent, sometimes warty (*T. longifolius*); style short, stigmas bifid into 2 arms. *Fruits* glabrous, warty or hairy; exocarp often partly detaching.

1. ***Trigonostemon longifolius*** Wall. ex Baill., Étude Euphorb. Atlas (1858) 23. pl. 11. f. 12, (‘*longifolium*’). — Lectotype (designated by Yu & van Welzen, 2018): *Wallich 7717* (lecto K, barcode K000959328; isolecto BR, barcode BR0000005105366, G-DC, barcode G00319787, GH, barcode GH00048885, K, barcode K000959327), Malaysia, Penang.

2. ***Trigonostemon merrillii*** Elmer, Leafl. Philipp. Bot. 4: 1304. 1911. — Type: *Elmer 12819* (BISH, barcode BISH1001684, BM, BO, accession BO1722342, F, barcode F0057180F, G, barcodes G00435100, G00435101, HBG, barcode HBG515778, L, barcode L0160280, MO, barcode MO260397, NY, barcode NY00273350, US, barcode US00096538), Philippines, Palawan, Puerto Princesa (Mt. Pulgar), Mar 1911.

3. ***Trigonostemon reidioides*** (Kurz) Craib, Bull. Misc. Inform., Kew (1911) 464. — Syntypes: *Teijsmann HB 5981* (K, barcode K000959313, U, barcode U.1260354), Thailand, Kanburi [= Kanchanaburi]; *Teijsmann s.n*. (CAL, barcode CAL0000023659), Thailand, Kanburi [= Kanchanaburi].

4. ***Trigonostemon sandakanensis*** Jabl., Brittonia 15: 159, f. 5, 6. — Type: *SAN* (*Wood*) *16018* (holo SING, barcode SING0051356; iso KEP, barcode KEP222404, L, barcode L.2258760), Malaysia, Sabah, Kabili-Sepilok Forest Reserve, 15 miles W of Sandakan, compartment 10, 15 ft above sea level, 21 Apr 1955.

The following species are not included in the molecular phylogeny but also belong to this section based on morphology:

5. ***Trigonostemon hybridus*** Gagnep., Bull. Soc. Bot. France 69 (1922) 750. — Type: *Pierre 6282* (P, barcode P00717109, other duplicates are syntypes of *T. rubescens*, see below), Vietnam, Phu-Quoc, Mar 1874.

6. ***Trigonostemon oblongifolius*** Merr., Philipp. J. Sci. 7 (1912) 409. — Type: *BS* (*Ramos*) *13965* (A bardcode A00048898, US, barcode US00096540), Philippines, Luzon, Cagayan, Abulug River, Feb 1912.

7. ***Trigonostemon rubescens*** Gagnep., Bull. Soc. Bot. France 69 (1922) 754. — Syntypes: *Pierre 6281* (P, barcodes P00717139, P00648668, P00648669, P00648670), Cambodia, Kompong Spen, Mont Ramcon, Jan 1870; *Pierre 6282* (K, barcode K000959312, P, barcodes P00717143, P00717144, P00717145), Vietnam, Phu-Quoc, Mar 1874; *Thorel 2290* (NY, barcode NY00273346, P, barcodes P00717140, P00717141, P00717142, US, barcode US00096544), Laos, Kong et île de Khon, 1866–1868.

3. ***Trigonostemon*** sect. ***Tylosepalum*** (Kurz) Benth. in Benth. & Hook.f., Gen. Pl. 3 (1880) 298.

Tylosepalum Kurz ex Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 27 (1864) 50. 1864. — *Codiaeum* A.Juss. sect. *Tylosepalum* (Kurz ex Teijsm. & Binn.) Müll.Arg. in A.DC., Prodr. 15 (1866) 1117. — *Trigonostemon* Blume sect. *Tylosepalum* (Kurz ex Teijsm. & Binn.) Pax & K.Hoffm. in Engl & Harms in Nat. Pflanzenfam. ed. 2, 19c (1931) 169. — Type: *Tylosepalum aurantiacum* Kurz ex Teijsm. & Binn. [= *Trigonostemon aurantiacus* (Kurz ex Teijsm. & Binn.) Boerl.].
Trigonostemon Blume sect. *Dichotomae* Merr., Univ. Calif. Publ. Bot. 10 (1924) 425. — Type: *Trigonostemon petelotii* Merr. [= *Trigonostemon laevigatus* Müll.Arg.].
Prosartema Gagnep., Bull. Soc. Bot. France 71 (1924b) 875. — Type: *Prosartema stellaris* Gagnep. [= *Trigonostemon stellaris* (Gagnep.) Airy Shaw].
Neotrigonostemon Pax & K.Hoffm., Notizbl. Bot. Gart. Berlin-Dahlem 10 (1928) 385. — Type: *Neotrigonostemon diversifolius* Pax & K.Hoffm. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].
Kurziodendron N.P.Balakr., Bull. Bot. Surv. India 8 (1966) 68. — Type: *Kurziodendron viridissimum* (Kurz) N.P.Balakr. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].

1. ***Trigonostemon albiflorus*** Airy Shaw, Kew Bull. 25 (1971) 547. — *Trigonostemon leucanthus* Airy Shaw var. *siamensis* H.S.Kiu in H.S.Kiu & X.X.Chen, Guihaia 12 (1992) 211. — Type: *Winit 1704* (syn K, barcodes K000959303, K000959304, isosyn BK, barcode BK257891, BM, barcode BM000951503), Thailand, Lampang, Mê Pêng, 110–200 m, evergreen forest, by stream, 19 Jun 1926.

2. ***Trigonostemon aurantiacus*** (Kurz ex Teijsm. & Binn.) Boerl., Handl. Fl. Ned. Ind. 3 (1900): 284. — Lectotype (designated by Yu & van Welzen, 2018): *Teijsmann s.n*. (lecto L, barcode L.2260196), Indonesia, Java, cultivated in Bogor Botanical Garden.

3. ***Trigonostemon bonianus*** Gagnep., Bull. Soc. Bot. France 69 (1922) 747. — Lectotype (designated by Li et al., 2006): *Bon 718* (lecto P, barcode P00717086), Vietnam, Mount Trui, 12 Sep 1881.

4. ***Trigonostemon cherrieri*** J.M.Veillon, Bull. Mus. Natl. Hist. Nat., B, Adansonia, sér. 4, 14 (1992) 55. — Type: *Veillon 7385* (holo P, barcode P00057693; iso K, barcode K000959366, L, barcode L0016479, P, barcodes P00057694, P00057695, P00057696, MO, barcode MO260396, NOU, barcodes NOU005872, NOU005874), New Caledonia, Poya, sud de Mepouiri, non loin de la côte, 10 m, Foret sclerophylle, en sous-bois, argiles noires tropicales, 25 Jun 1991.

5. ***Trigonostemon hartleyi*** Airy Shaw, Kew Bull. 33 (1979) 535. — Type: *Hartley 11087* (holo BRI, barcode BRI-AQ0342687; iso L, barcode L0043309), New Guinea, Morobe, Busu, S of the Busu River, c. 12 miles N of Lae, 500 ft, rainforest on slope, 8 Jan 1963.

6. ***Trigonostemon inopinatus*** Airy Shaw, Kew Bull. 31 (1976) 396. — Type: *Webb & Tracey 7762* (holo BRI, barcode BRI-AQ0205473, on 2 sheets), Australia, Queensland, Cawley State Forest west of Cathu between Mackay & Proserpine, 2000 ft, rainfall 70 inch, mixed notophyll vine forest on soils derived from granite, Jun 1965.

7. ***Trigonostemon laevigatus*** Müll.Arg., Flora 47 (1864b) 538. — Lectotype (designated by Yu & van Welzen, 2018): *Motley 686* (lecto K, barcode K000959291), Indonesia, South Kalimantan, Bangarmassing [= Banjarmasin], 1857–1858.

8. ***Trigonostemon lii*** Y.T.Chang, Guihaia 3 (1983) 175. — Type: *Li 4576* (holo KUN, barcode KUN1294357), China, Yunnan, Xishuangbanna Botanical Garden, on limestone hill, 25 Jun 1963.

9. ***Trigonostemon philippinensis*** Stapf, Leafl. Philipp. Bot. 1 (1907) 206, ('*philippinense*'). — Type: *Elmer 8326* (BO, accession BO1298668, G, barcode G00435099, K, barcode K000959370, L, barcode L.2260355), Philippines, Luzon, Laguna, Los Baños, May 1906.

10. ***Trigonostemon quocensis*** Gagnep., Bull. Soc. Bot. France 69 (1922) 753. — Syntypes: *Pierre s.n*. (K, barcode K000959314, P, barcodes P00717135, P00717136, P00717138), Vietnam, Phu Quoc, Mar 1874; *Godefroy 739* (P, barcode P00717131, P00717132), Vietnam, Ha-tien, 20 Sep 1875; *Godefroy 740* (P, barcode P00717130), Vietnam, Ha-tien, 20 Sep 1875; *Pierre 6232* (G, barcode G00435097, P, barcodes P00717133, P00717134, P00717137, MPU, barcodes MPU015001, MPU015002, NY barcode NY00273345), Vietnam, Chaudoc, Mount Pell, Dec 1867; *Harmand 632* (P, barcodes P00717128, P00717129), Vietnam, Nui Cam, Jun 1876.

11. ***Trigonostemon viridissimus*** (Kurz) Airy Shaw, Kew Bull. 25 (1971) 545. — Type: *Kurz s.n*. (K, barcodes K000246871, K000246871), India, South Andaman, Port Mouat.

12. ***Trigonostemon verrucosus*** J.J.Sm., Bull. Jard. Bot. Buitenzorg ser. 3, 6 (1924) 97. — Type: *Bogor Botanical Garden VIII.E.16* (BO, accessions BO1298241, BO1298242, BO1298243, IBSC, barcode IBSC0306957, K, barcode K000959299, L, barcode L.2258669, SING, U, barcode U0002105), Cultivated in Bogor Botanical Garden, 20 May 1896.

13. ***Trigonostemon wui*** H.S.Kiu, J. Trop. & Subtrop. Bot. 3 (1995) 19, f. 2. — Type: *Kiu 451* (holo IBSC, not found; iso IBK, barcode IBK00190788), China, Guangdong, Fengkai, Yulao, 80 m, foot of limestone hill, 12 May 1995.

14. ***Trigonostemon xyphophylloides*** (Croizat) L.K.Dai & T.L.Wu, Acta Phytotax. Sin. 8 (1963) 277. — Type: *Wang 34005* [cited as '*34006*' in Croizat 1940, probably a typo; marked as holotype in A by L.C.M. Croizat] (A, barcode A00045961, IBK, barcode IBK00169539, IBSC, K, barcode K000959334), China, Hainan, Ya County, in dense forest, 17 Sep 1933.

The following species are not included in the molecular phylogeny but also belong to this section based on morphology:

15. ***Trigonostemon adenocalyx*** Gagnep., Bull. Soc. Bot. France 69 (1922) 747. — Type: *Unknown collector* (P, barcode P00717084), Indochina?

16. ***Trigonostemon apetalogyne*** Airy Shaw, Kew Bull. 33 (1979) 534. — Type: *Kostermans & Soegeng 340* (holo K; iso BO), Indonesia, West Papua, limestone hills E of Sukarnapura [= Hollandia = Djajapura], Polima I, c. 100 m, 13 Aug 1966.

17. ***Trigonostemon birmanicus*** Chakrab. & N.P.Balakr., J. Econ. Taxon. Bot. 5 (1984a) 175. —Type: *Chin* [collector's name uncertain] *5849* (holo CAL, barcode CAL0000023654), Myanmar, Upper Chindwin, Numpakom drainage, 1400 ft, on loamy soil, 29 Apr. 1911.

18. ***Trigonostemon capitellatus*** Gagnep., Bull. Soc. Bot. France 69 (1922) 748. — Syntypes: *Thorel s.n*. (P, barcode P00717089), Laos, Île de Khon, 1866–1868; *Pierre 472* (P, barcode P00717093), Vietnam, ad flumen Dongnai prope Tri Huyen in prov. Bien Hoa, Sep 1869; *Pierre 1323* (K, barcode K000959315, P, barcodes P00717090, P00717091, P00717092, US00433339), Vietnam, ad flumen Dongnai prope Tri Huyen in prov. Bien Hoa, Mar 1873.

19. ***Trigonostemon cochinchinensis*** Gagnep., Bull. Soc. Bot. France 69 (1922) 748. — Type: *Pierre 1869* (K, barcode K000959316, P, barcodes P00717094, P00717095, P00717096), Vietnam, Bao Chiang, Jul 1877.

20. ***Trigonostemon chinensis*** Merr., Philipp. J. Sci., Bot. 21 (1922) 498. — Type: *Tsoong* (PE, barcode PE01110916, PNH, accession 88948), China, Guangxi, Tung Sing [= Dongxing], Dongjingshan, 21 [22 in protologue] Jun 1918.

21. ***Trigonostemon eberhardtii*** Gagnep, Bull. Soc. Bot. France 69 (1922) 749. — Syntypes: *Bon 5239* (P, barcode P00717103), Vietnam, Annam, Thanh-hoa; *Bon 5465* (P, barcodes P00717099, P00717100) , Vietnam, Annam, Son-thôn; *Eberhardt 4293* (P, barcodes P00717101, P00717102), Vietnam, Tonkin, Hoa-binh, Mai-ha.

22. ***Trigonostemon fragilis*** (Gagnep.) Airy Shaw, Kew Bull. 32 (1978): 415. — Type: *Poilane 2927* (A, barcode A00106974, P, barcodes P00712172, P00712173, P00712174), Vietnam, Annam, Île Tre près de Nhatrang, 10 Apr 1922.

23. ***Trigonostemon harmandii*** Gagnep., Bull. Soc. Bot. France 69 (1922) 750. — Type: *Harmand 2956* (P, barcodes P00648665, P00648666, P00648667), Cambodia, 1875–1877.

24. ***Trigonostemon heteranthus*** Wight, Icon. Pl. Ind. Orient. 5 (1852) 24, t. 1890. — Syntypes: *Griffith s.n*. (K, barcode K000246861), Myanmar, Mergui; *Griffith KD 4796* (K, barcode K000246910, P, barcode P00717107), Myanmar, Mergui; *Helfer KD 4796* (K, barcode K000246862), Myanmar, Mergui.

25. ***Trigonostemon nigrifolius*** N.P.Balakr. & Chakrab., J. Econ. Taxon. Bot. 5 (1984b) 173. — Type: *Po Khaut 12434* (holo DD), Myanmar, Maymyo, Gokteik viaduct, 16 May 1929.

26. ***Trigonostemon poilanei*** Gagnep., Bull. Soc. Bot. France 69 (1922) 753. — Type: *Poilane* [*Chevalier* & *Poilane* in protologue] *40807* (A, barcode A00048878, P, barcode P00717127), Vietnam, Bienhoa, Giaray, 22 May 1919.

27. ***Trigonostemon thorelii*** Gagnep., Bull. Soc. Bot. France 69 (1922) 755. — Type: *Thorel 2264* (A, barcode A00048877, P, barcodes P00648671, P00648672, P00717148), Laos, Stung Tréng à Kong, 1866–1868.

28. ***Trigonostemon tuberculatus*** F.Du & Ju He, Kew Bull. 65 (2010) 111, f. 1, 2. — Type: *Du*, *He* & *Zhang 200401* (holo SWFC), China, Yunnan, Yuanjiang, 460 m, in secondary shrub on slope of dry hill, 1 May 2004.

4. ***Trigonostemon*** Blume sect. ***Pycnanthera*** Benth., J. Linn. Soc., Bot. 17 (1878) 225. — Lectotype (designated by Yu & van Welzen 2018): *Trigonostemon diplopetalus* Thwaites.

Nepenthandra S.Moore in J. Bot. 43 (1905) 149. — Type: *Nepenthandra lanceolata* S.Moore [= *Trigonostemon lanceolatus* (S.Moore) Pax].

1. ***Trigonostemon diplopetalus*** Thwaites, Enum. Pl. Zeyl. (1861) 277. — Type: *Thwaites CP 578* (A, barcode A00048867, BR, barcode BR0000005105045, CAL, barcodes CAL0000023676, CAL0000023677, FR, barcode FR0036073, G, barcode G00435106, G-DC, barcode G00319791, GH, barcode GH00048868, P, barcodes P00717097, P00717098, K, barcode K000246865), Sri Lanka, Reigam Corle, Palahattoo, at no great elevation, Sep 1858.

2. ***Trigonostemon nemoralis*** Thwaites, Enum. Pl. Zeyl. (1861) 277. — Types: *Thwaites CP 3570* (A, barcode A00048874, CAL, barcodes CAL0000023670, CAL0000023671, FR, barcode FR0036074, G-DC, barcodes G00319812, G00319788, GH, barcode GH00048873, K, barcodes K000246866, K000246867, K000246868, K000246869, NY, barcode NY00273343, P, barcodes P00717116, P00717117, P00717118), Sri Lanka, Central Province, Madamahanewera, 2000 ft.

Taxonomic treatment of *Tritaxis*

Taxonomic treatment of *Dimorphocalyx* spp. is based on van Welzen & van Oostrum (2015), Chakrabarty & Balakrishnan (1990), Venkata Raju & Pullaiah (1994), Gagnepain (1924a) and Pax & Hoffmann (1924); only the protologue of each taxon is given.

Tritaxis Baill., Étude Euphorb. (1858) 342. — Type: *Tritaxis gaudichaudii* Baill.
Dimorphocalyx Thwaites, Enum. Pl. Zeyl. (1861) 278. — *Trigonostemon* Blume sect. *Dimorphocalyx* (Thwaites) Müll.Arg., Linnaea 34 (1865) 212. — Type: *Dimorphocalyx glabellus* Thwaites.

1. ***Tritaxis australiensis*** S.Moore, J. Linn. Soc., Bot. 45 (1920) 218. — Type: *Damel s.n.* (BRI, barcode BRI-AQ0202253, K, barcode K000894750), Australia, Queensland, Cape York, Cook pastoral district, Mar 1868.
Dimorphocalyx australiensis C.T.White, Proc. Roy. Soc. Queensl. 47 (1936) 80. — Type: *Brass 2019* (holo BRI, barcode BRI-AQ0342526; iso A, barcode A00047607, K, barcode K000894749, US, barcode US01108415), Australia, Queensland, Mowbray River, Rainforest, 23 Jan 1932.

2. ***Tritaxis balakrishnanii*** (Chakrab. & Premanath) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx balakrishnanii* Chakrab. & Premanath, J. Econ. Taxon. Bot. 4 (1983) 1013. —Type: *Ansari 1368A* (holo CAL), India, Andaman-Nicobar Islands, Havelock Island, 40 m, 15 May 1874; *Ansari 1368B* (iso PBL), India, Andaman-Nicobar Islands, Havelock Island, 40 m, 15 May 1874; *Ansari 1368C* (iso PBL), India, Andaman-Nicobar Islands, Havelock Island, 40 m, 15 May 1874; *Ansari 1368D* (iso PBL), India, Andaman-Nicobar Islands, Havelock Island, 40 m, 15 May 1874; *Ansari 1368E* (iso PBL), India, Andaman-Nicobar Islands, Havelock Island, 40 m, 15 May 1874.
   Dimorphocalyx dilipianus N.P.Balakr. & Chakrab., J. Econ. Taxon. Bot. 4 (1983) 1017. — Type: *Nair 498A* (holo CAL), India, Andaman-Nicobar Islands, South Andaman Island, Carbyn's Cove, c. 20 m, 10 Oct 1973; *Nair 498B* (iso PBL), India, Andaman-Nicobar Islands, South Andaman Island, Carbyn's Cove, c. 20 m, 10 Oct 1973; *Nair 498C* (iso PBL), India, Andaman-Nicobar Islands, South Andaman Island, Carbyn's Cove, c. 20 m, 10 Oct 1973; *Nair 498D* (iso PBL), India, Andaman-Nicobar Islands, South Andaman Island, Carbyn's Cove, c. 20 m, 10 Oct 1973; *Nair 498E* (iso PBL), India, Andaman-Nicobar Islands, South Andaman Island, Carbyn's Cove, c. 20 m, 10 Oct 1973.

3. ***Tritaxis beddomei*** Benth., J. Linn. Soc., Bot. 17 (1878) 221. — *Dimorphocalyx beddomei* (Benth.) Airy Shaw in Kew Bull. 23 (1969) 124. — Type: *Beddome 37* (K, barcode K000246899), India, Tinnevelly.

4. ***Tritaxis cumingii*** (Müll.Arg.) Benth., J. Linn. Soc., Bot. 17 (1878) 221. — *Trigonostemon cumingii* Müll.Arg., Linnaea 34 (1865) 213. — *Dimorphocalyx cumingii* (Müll.Arg.) Airy Shaw, Kew Bull. 23 (1969) 124. — Type: *Cuming 1693* (holo G-DC, barcode G00319795; iso BM, barcodes BM000951496, BM000951497, E, barcode E00570192, G, barcode G00435094, K, barcodes K000959395, K000959396, L, barcodes L0016166, L0016167, P, barcode P00640260), Philippines, 1841.

5. ***Tritaxis denticulatus*** (Merr.) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx denticulatus* Merr., Philipp. J. Sci. 4 (1909) 278. — Type: *FB* (*Whitford* & *Hutchinson*) *9033* (K, barcode K000959394, US, barcode US00096562), Philippines, Mindanao, Zamboanga, Port Banga, 30 m, in dipterocarp forests, Nov–Dec 1907.
   Dimorphocalyx murinus Elmer, Leafl. Philipp. Bot. 4 (1911) 1285, ('*murina*'). — Lectotype (designated by van Welzen & van Oostrum, 2015): *Elmer 12844* (lecto L, barcode L0245421; isolecto BM, G, barcode G00434828, GH, barcode GH00047605, HBG, barcode HBG516375, K, barcode K000959390, L, barcode L0245421, NY, barcode NY00804228, P, barcode P00712200, U, barcode U0226764, US, barcode US00731069), Philippines, Palawan, Puerto, Princesa (Mt. Pulgar), Mar 1911.
   Dimorphocalyx loheri Merr., Philipp. J. Sci. 27 (1925) 30. — Lectotype (designated by van Welzen & van Oostrum, 2015): *Loher 12467* (lecto UC, barcode UC241187; isolecto A, barcode A00047604), Philippines, Luzon, Rizal, Montalban., Jun 1909.

6. ***Tritaxis gaudichaudii*** Baill., Étude Euphorb. (1858) 343. — Lectotype (designated here): *Gaudichaud 278* (lecto P, barcode P00712262; isolecto P, barcodes P00712260, P00712261), Vietnam, 1836–1837. Other syntypes: *Gaudichaud 296* (P, barcodes P00712258, P00712259), Vietnam, 1836–1837.

7. ***Tritaxis glabellus*** (Thwaites) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx glabellus* Thwaites, Enum. Pl. Zeyl. (1861) 278. — Type: *Thwaites C.P. 1046* (BR, barcode BR0000005101849, FR, barcode FR0031457, G, barcode G00434940, P, barcodes P00712195, P00712196, P00712197), Sri Lanka.

7a. ***Tritaxis glabellus*** (Thwaites) R.Y.Yu & Welzen var. ***glabellus***

7b. ***Tritaxis glabellus*** (Thwaites) R.Y.Yu & Welzen var. ***lawianus*** (Nimmo) R.Y.Yu & Welzen, *comb. nov.* — *Croton lawianus* Nimmo, Cat. Pl. Bombay (1839) 251. — *Trigonostemon lawianus* (Nimmo) Müll.Arg., Linnaea 34 (1865) 212. — *Dimorphocalyx lawianus* (Nimmo) Hook.f., Fl. Brit. India 5 (1887) 404. — *Dimorphocalyx glabellus* Thwaites var. *lawianus* (Nimmo) Chakrab. & N.P.Balakr., Proc. Indian Acad. Sci (Plant Sci) 100 (1990) 296. — Type: *Gibson 19* (K, barcode K000246856), India, Bombay, Bheema Snnker.

8. ***Tritaxis ixoroides*** (C.B.Rob.) R.Y.Yu & Welzen, *comb. nov.* — *Ostodes ixoroides* C.B.Rob., Philipp. J. Sci. 6 (1911) 332. — *Dimorphocalyx ixoroides* (C.B.Rob.) Airy Shaw, Kew Bull. 20 (1967) 412. — Type: *FB* (*Klemme*) *13426* (US, barcode US00096560), Philippines, Luzon, Ilocos Norte, Bangui, Apr 1909.

9. ***Tritaxis kurnoolensis*** (R.R.V.Raju & Pull.) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx kurnoolensis* R.R.V.Raju & Pull., Bot. Bull. Acad. Sin. 35 (1994) 201. — Type: *Venkata Raju 6661* (holo MH; iso SKU), India, Andhra Pradesh, Kurnool, Owk stream.

10. ***Tritaxis malayanus*** (Hook.f.) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx malayanus* Hook.f., Fl. Brit. India 5 (1887) 404. — Lectotype (designated by van Welzen & van Oostrum, 2015): *Griffith KD 4785* (lecto K, barcode K000894751; isolecto A, barcode A00139220, P, barcode P00648681), Malaysia, Malacca.
Dimorphocalyx kunstleri King ex Hook.f., Fl. Brit. India 5 (1887) 405. — Type: *King's collector 1455* (K, barcode K000894756), Malaysia, Penang, Mar 1881.
Dimorphocalyx luzoniensis Merr., Philipp. J. Sci. 5 (1910) 192. — Lectotype (designated by van Welzen & van Oostrum, 2015): *FB* (*Tamesis*) *11907* (lecto K, barcode K000959392; isolecto US, barcode US00096564), Philippines, Luzon, Prov. of Laguna, Los Baños, 22 Jan, 1910.
Dimorphocalyx beccarii Gagnep., Bull. Soc. Bot. France 71 (1924a) 621. — Lectotype (designated by van Welzen & van Oostrum, 2015): *Beccari PB 2215* (lecto P, barcode P00648685; isolecto A, barcode A00047603, K, barcodes K000959398, K000959400), Malaysia, Sarawak.
Trigonostemon bulusanensis Elmer, Leafl. Philipp. Bot. 10 (1939) 3735. — *Dimorphocalyx bulusanensis* (Elmer) Airy Shaw, Kew Bull. 27 (1972b) 92. — Type: *Elmer 17296* (G, barcode G00435102, HBG, barcode HBG515781, L, barcode L.2204370, MO, barcode MO260399, NY, barcode NY00179801, S, accession S07-17047, U, barcode U0226748), Philippines, Luzon, Sorsogon, Irosin (Mt. Bulusan), 2000 ft, in well shaded woods.

11. ***Tritaxis meeboldii*** (Pax & K.Hoffm.) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx meeboldii* Pax & K.Hoffm. in Engl., Pflanzenr. IV. 147 xvi (1924) 190. — Type: *Meebold 16837* (?), Myanmar, Moulmein, Papun.

12. ***Tritaxis moluccensis*** (Welzen & Oostrum) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx moluccensis* Welzen & Oostrum, Blumea 59 (2015) 198. — Type: *de Vogel 3134* (holo L, barcode L.2204209), Indonesia, N Moluccas, Halmahera, Ekor, side of Gunung Panjang, c. 0°49' N, 127°52'E, 15 m, rather dense primary forest 35 m high, with little undergrowth, rather steep hill side on deep clay soil, 27 Sep 1974.

13. ***Tritaxis muricatus*** (Hook.f.) R.Y.Yu & Welzen, *comb. nov.* — *Ostodes muricata* Hook.f., Fl. Brit. India 5 (1887) 401. — *Ostodes muricata* Hook.f. var. *genuina* Pax in Pax & K.Hoffm. in Engl., Pflanzenr. IV.147 iii (1911) 21, nom. inval. — *Dimorphocalyx muricatus* (Hook.f.) Airy Shaw, Kew Bull. 20 (1967) 412. — Type: *King's collector 3162* (K, barcode K000894757), Malaysia, Perak, Larut, within 500 ft, dense jungle, Aug 1882.
Trigonostemon asahanensis Croizat, J. Arnold Arbor. 23 (1942a) 54. — Type: *Rahmat Si Boeea 9872* (holo A, barcode A00048880; iso L, barcode L.2204342), Indonesia, Sumatra, Asahan, vicinity of Tomoean Dolok, c. 1000m, 1–20 Aug 1936.
Ostodes muricata Hook.f. var. ? *minor* Hook.f., Fl. Brit. India 5 (1887) 401. — *Dimorphocalyx muricatus* (Hook.f.) Airy Shaw var. *minor* (Hook.f.) Airy Shaw, Kew Bull. 20 (1967) 412. — Lectotype (designated by van Welzen & van Oostrum, 2015): *Lobb 304* (lecto BM, barcode BM000541792; isolecto E, barcode E00314237, GH, barcodes GH00139221, GH00139222, K, barcode K000894761, L, barcode L0245384), Singapore.

14. ***Tritaxis pauciflorus*** (Merr.) R.Y.Yu & Welzen, *comb. nov.* — *Ostodes pauciflorus* Merr., Philipp. J. Sci. 11 (1916a) 72. — *Dimorphocalyx pauciflorus* (Merr.) Airy Shaw, Kew Bull. 20 (1967) 413. — Type: *Hose 244* (A, barcode A00048886, K, barcodes K000959402, K000959403, L, barcode L0016394, P, barcode P00648684), Malaysia, Sarawak, Baram District, Baram, Mar 1895.

15. ***Tritaxis poilanei*** (Gagnep.) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx poilanei* Gagnep., Bull. Soc. Bot. France 71 (1924a) 622. — Type: *Poilane 4786* (A, barcode A00135094, K, barcode K000959404, P, barcodes P00648682, P00648683), Vietnam, Annam, Nui Han Heo près de Nhatrang, sol rocheux, forêt, 300 m, 28 Sep 1922.

16. ***Tritaxis trichocarpus*** (Airy Shaw) R.Y.Yu & Welzen, *comb. nov.* — *Dimorphocalyx trichocarpus* (Airy Shaw) Welzen & Oostrum, Blumea 59 (2015) 199. — *Dimorphocalyx luzoniensis* Merr. var. *trichocarpus* Airy Shaw, Kew Bull., Addit. Ser. 4 (1975) 96. — Type: *S* (*Anderson*) *20974* (holo K, barcode K000959401; iso L, barcode L.2182719), Malaysia, Sarawak, First Division, Bidi, Bau, 300 ft, on limestone rocks, with intervening igneous derived soil, at base of limestone hill, 12 Apr 1965.

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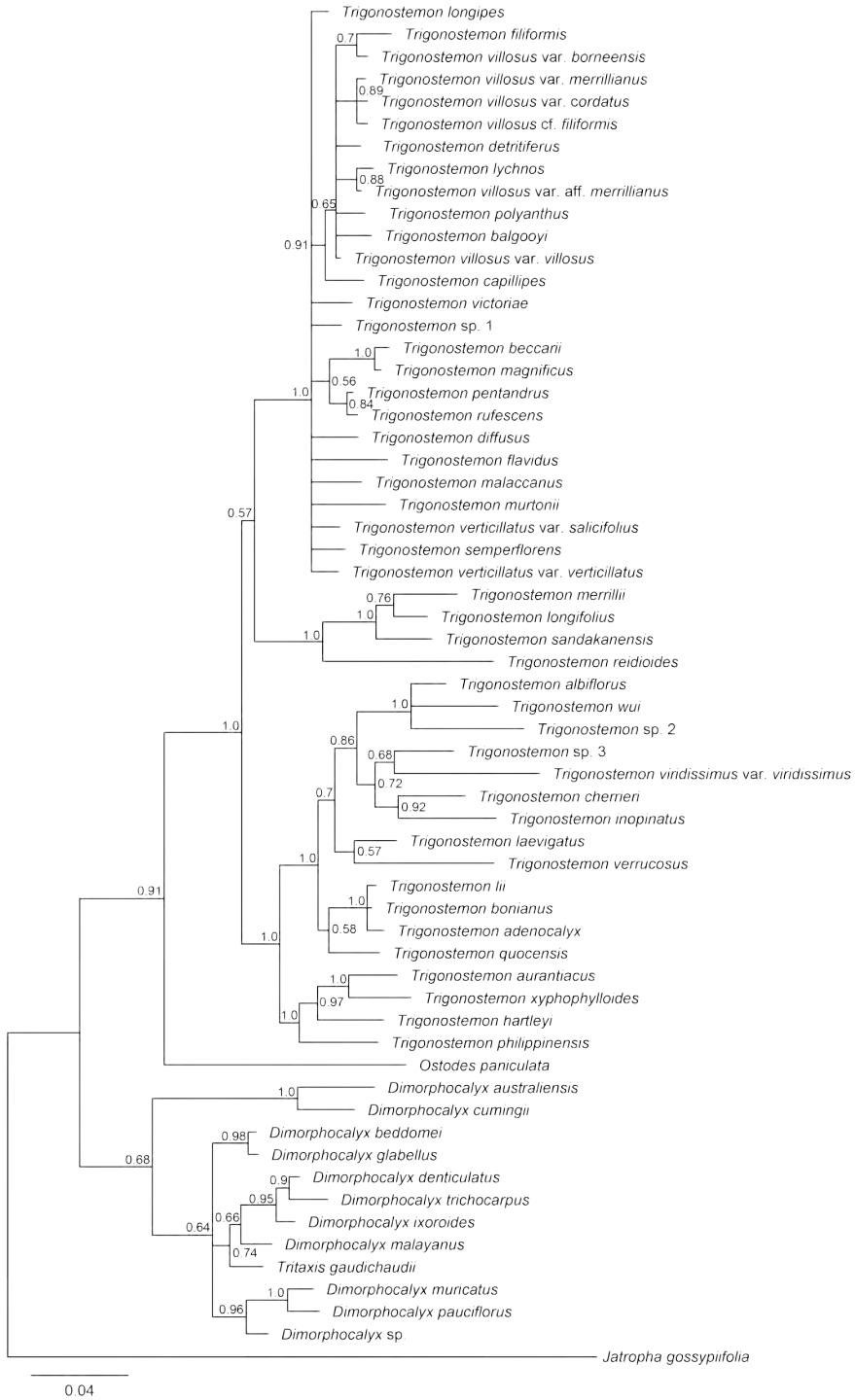
Research Institute Malaysia), Maribel E. Agoo (De La Salle University, Manila, the Philippines) and John Rey Callado (National Museum of the Philippines) are thanked for their assistance with the field work. The last author thanks the Treub-Maatschappij for supporting the Ornstein chair in Tropical Plant Biogeography.

Supplementary material



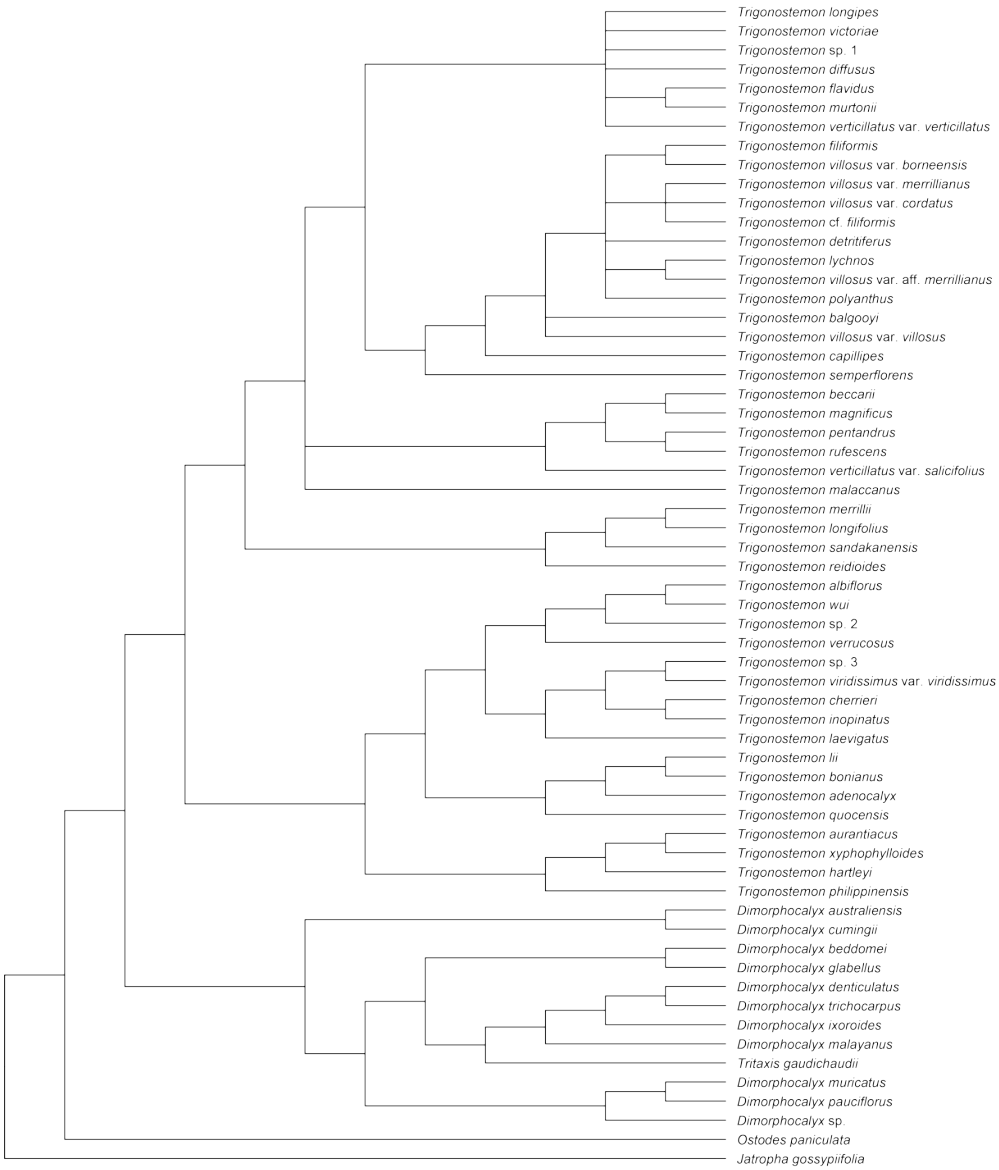
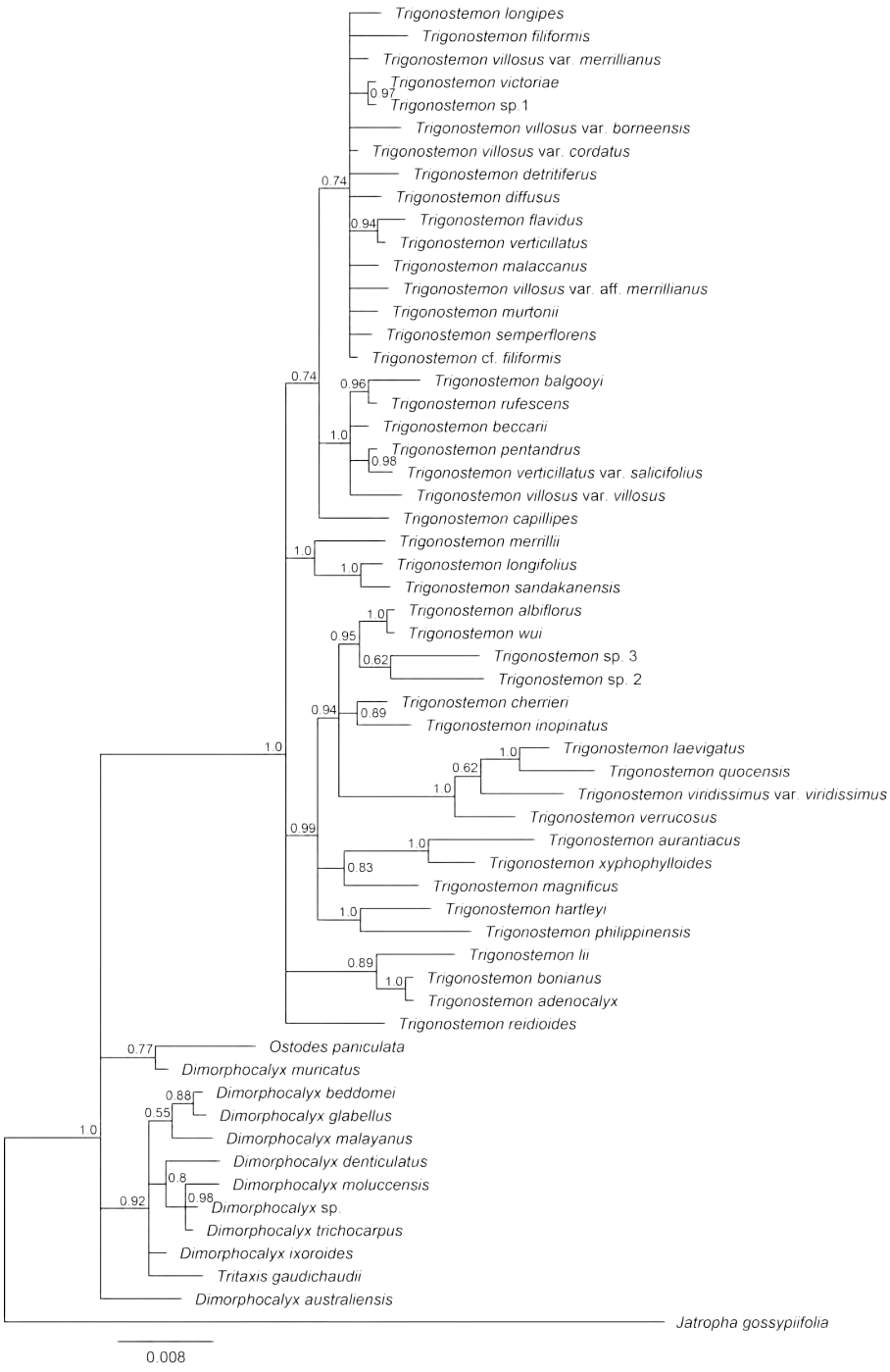


Figure 44 Phylogenetic relationship of selected species of *Trigonostemon*, *Dimorphocalyx*, *Ostodes* and *Tritaxis* using the maximum parsimony method. The phylogram was reconstructed based on the nuclear ITS sequence. The 50% consensus of the best-scored trees is shown.

←

Figure 43 Phylogenetic relationship of selected species of *Trigonostemon*, *Dimorphocalyx*, *Ostodes* and *Tritaxis* using the Bayesian inference method. The phylogram was reconstructed based on the nuclear ITS sequence. The numbers next to the clades are the posterior probability from the BI analysis. The clades are omitted if the posterior probability is below 0.55.


Trigonostemon longipes
Trigonostemon filiformis
Trigonostemon villosus var. merrillianus
Trigonostemon victoriae
Trigonostemon sp.1
Trigonostemon villosus var. borneensis
Trigonostemon villosus var. cordatus
Trigonostemon detritiferus
Trigonostemon diffusus
Trigonostemon flavidus
Trigonostemon verticillatus
Trigonostemon malaccanus
Trigonostemon villosus var. aff. merrillianus
Trigonostemon murtonii
Trigonostemon semperflorens
Trigonostemon cf. filiformis
Trigonostemon balgooyi
Trigonostemon rufescens
Trigonostemon beccarii
Trigonostemon pentandrus
Trigonostemon verticillatus var. salicifolius
Trigonostemon villosus var. villosus
Trigonostemon capillipes
Trigonostemon merrillii
Trigonostemon longifolius
Trigonostemon sandakanensis
Trigonostemon albiflorus
Trigonostemon wui
Trigonostemon sp. 3
Trigonostemon sp. 2
Trigonostemon cherrieri
Trigonostemon inopinatus
Trigonostemon laevigatus
Trigonostemon quocensis
Trigonostemon viridissimus var. viridissimus
Trigonostemon verrucosus
Trigonostemon aurantiacus
Trigonostemon xyphophylloides
Trigonostemon magnificus
Trigonostemon hartleyi
Trigonostemon philippinensis
Trigonostemon lii
Trigonostemon bonianus
Trigonostemon adenocalyx
Trigonostemon reidioides
Ostodes paniculata
Dimorphocalyx muricatus
Dimorphocalyx beddomei
Dimorphocalyx glabellus
Dimorphocalyx malayanus
Dimorphocalyx denticulatus
Dimorphocalyx moluccensis
Dimorphocalyx sp.
Dimorphocalyx trichocarpus
Dimorphocalyx ixoroides
Tritaxis gaudichaudii
Dimorphocalyx australiensis
Jatropha gossypiifolia
0.008

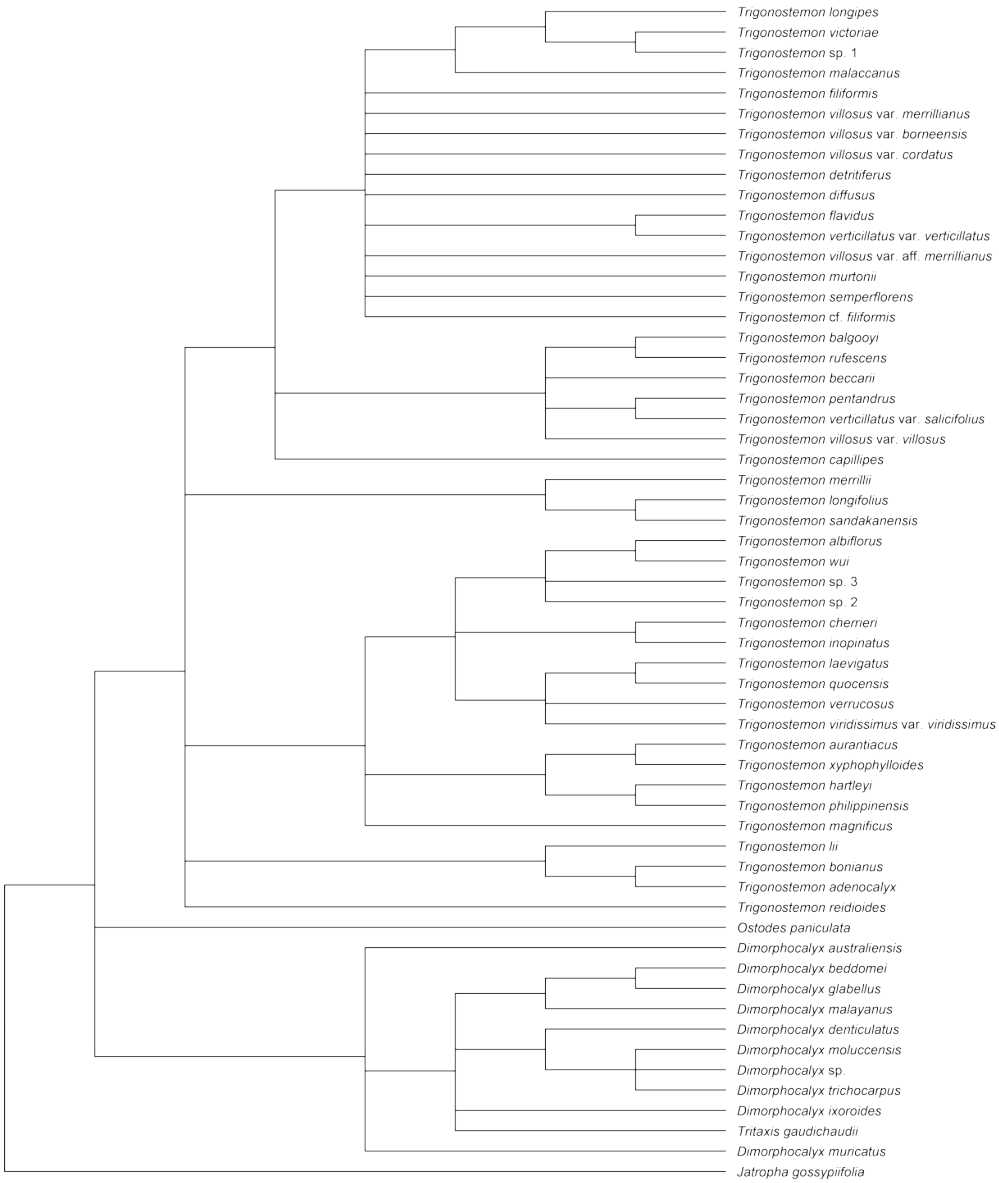
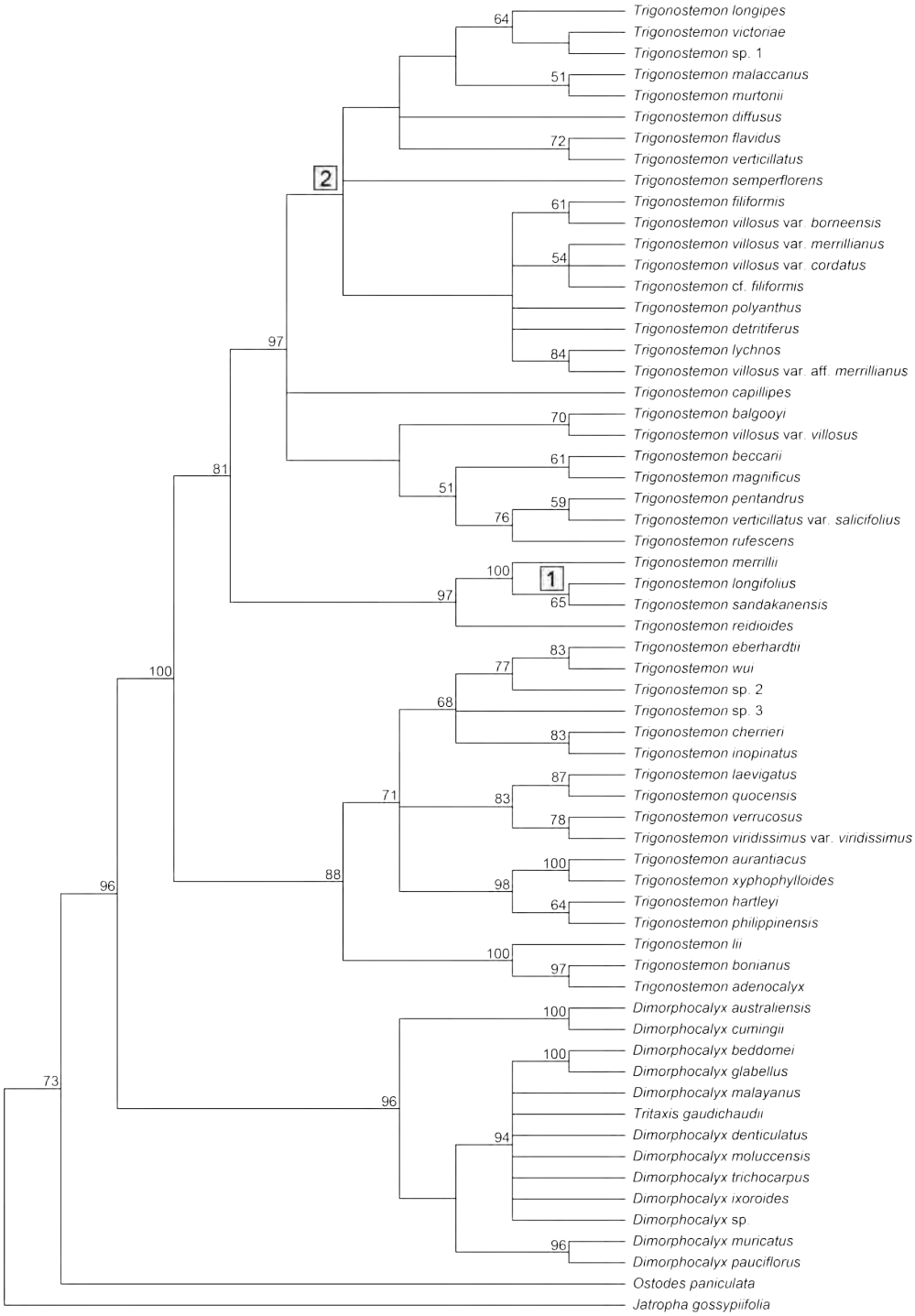


Figure 46 Phylogenetic relationship of selected species of *Trigonostemon*, *Dimorphocalyx*, *Ostodes* and *Tritaxis* using the maximum parsimony method. The phylogram was reconstructed based on the chloroplast *trnK* intron, *trnT-L* and *trnL-F* sequences.The 50% consensus of the best-scored trees is shown.

←

Figure 45 Phylogenetic relationship of selected species of *Trigonostemon*, *Dimorphocalyx*, *Ostodes* and *Tritaxis* using the Bayesian inference method. The phylogram was reconstructed based on the chloroplast *trnK* intron, *trnT-L* and *trnL-F* sequences. The numbers next to the clades are the posterior probability from the BI analysis. The clades are omitted if the posterior probability is below 0.55.


Trigonostemon longipes
Trigonostemon victoriae
Trigonostemon sp. 1
Trigonostemon malaccanus
Trigonostemon murtonii
Trigonostemon diffusus
Trigonostemon flavidus
Trigonostemon verticillatus
Trigonostemon semperflorens
Trigonostemon filiformis
Trigonostemon villosus var. borneensis
Trigonostemon villosus var. merrillianus
Trigonostemon villosus var. cordatus
Trigonostemon cf. filiformis
Trigonostemon polyanthus
Trigonostemon detritiferus
Trigonostemon lychnos
Trigonostemon villosus var. aff. merrillianus
Trigonostemon capillipes
Trigonostemon balgooyi
Trigonostemon villosus var. villosus
Trigonostemon beccarii
Trigonostemon magnificus
Trigonostemon pentandrus
Trigonostemon verticillatus var. salicifolius
Trigonostemon rufescens
Trigonostemon merrillii
Trigonostemon longifolius
Trigonostemon sandakanensis
Trigonostemon reidioides
Trigonostemon eberhardtii
Trigonostemon wui
Trigonostemon sp. 2
Trigonostemon sp. 3
Trigonostemon cherrieri
Trigonostemon inopinatus
Trigonostemon laevigatus
Trigonostemon quocensis
Trigonostemon verrucosus
Trigonostemon viridissimus var. viridissimus
Trigonostemon aurantiacus
Trigonostemon xyphophylloides
Trigonostemon hartleyi
Trigonostemon philippinensis
Trigonostemon lii
Trigonostemon boniianus
Trigonostemon adenocalyx
Dimorphocalyx australiensis
Dimorphocalyx cumingii
Dimorphocalyx beddomei
Dimorphocalyx glabellus
Dimorphocalyx malayanus
Tritaxis gaudichaudii
Dimorphocalyx denticulatus
Dimorphocalyx moluccensis
Dimorphocalyx trichocarpus
Dimorphocalyx ixoroides
Dimorphocalyx sp.
Dimorphocalyx muricatus
Dimorphocalyx pauciflorus
Ostodes paniculata
Jatropha gossypiifolia
1
2
64
51
72
61
54
84
70
61
51
59
76
100
97
65
83
77
68
83
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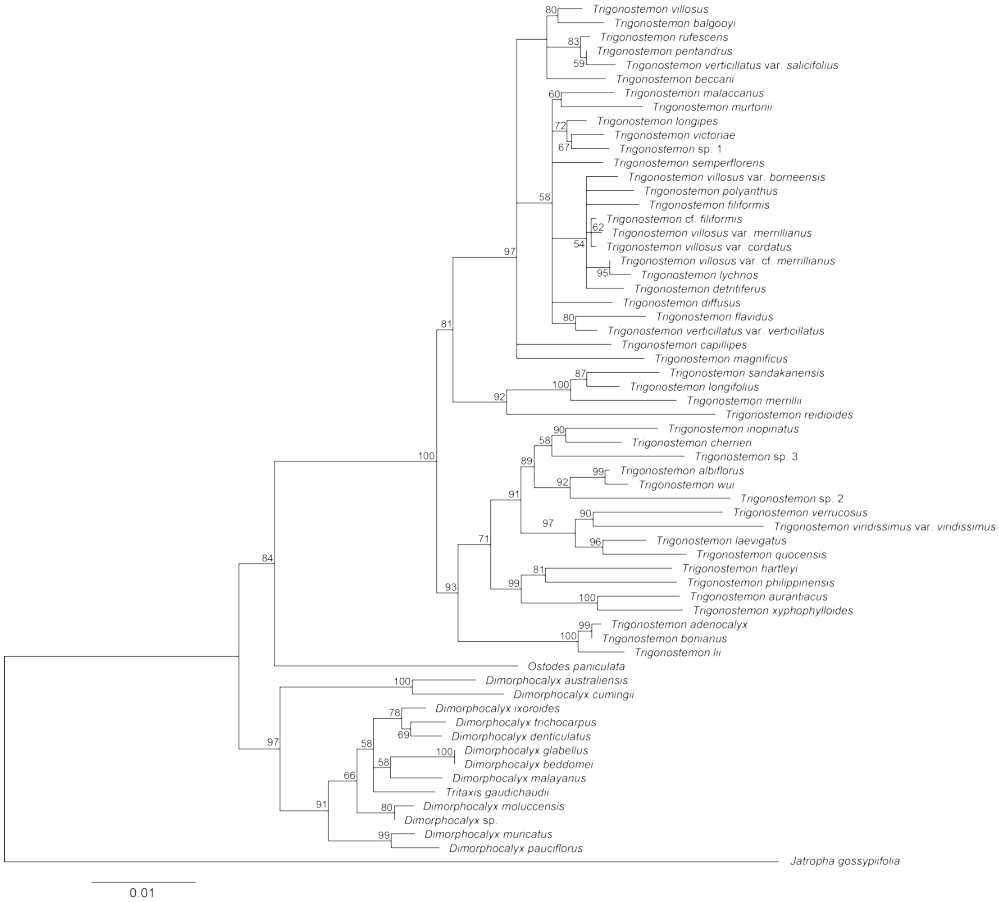

Figure 48 Phylogenetic relationship of selected species of *Trigonostemon*, *Dimorphocalyx*, *Ostodes* and *Tritaxis* based on the nuclear ITS and the chloroplast *trnK* intron, *trnT-L* and *trnL-F* sequences. The phylogram was reconstructed using the maximum likelihood method. The numbers next to the clades are the bootstrap supports. The clades are omitted if the bootstrap support is below 50.

←

Figure 47 Phylogenetic relationship of selected species of *Trigonostemon*, *Dimorphocalyx*, *Ostodes* and *Tritaxis* using based on the nuclear ITS and the chloroplast *trnK* intron, *trnT-L* and *trnL-F* sequences. The phylogram was reconstructed using the maximum parsimony method. The 50% consensus of the best-scored trees is shown. The bootstrap support are shown next to nodes if the value is above 50. Two major parsimony informative indels are marked on the phylogram.

Chapter 7 Historical biogeography of *Trigonostemon* and *Dimorphocalyx* (Euphorbiaceae)

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Abstract *Trigonostemon* and *Dimorphocalyx* are two morphologically similar genera in tropical Asia. We estimated their divergence times through a Bayesian clock analysis and reconstructed the historical biogeography using a likelihood analysis under the Dispersal-Extinction-Cladogenesis (DEC) model and a Statistical Dispersal-Vicariance analysis (S-DIVA). We have found that the two genera differ in their historical biogeography: *Trigonostemon* originated on SE Asian mainland, but one section dispersed to the Malay Peninsula and Borneo, where rapid speciation events occurred during the Pleistocene, whereas *Dimorphocalyx* originated and extended to its current distribution from Borneo. The dispersal routes of both genera are well supported by the tectonic history and are comparable to the conclusions in previous case studies. Long-distance dispersals across Wallace's line are of particular interest in biogeography. Our data support the hypothesis that the Philippines is the most often used stepping stone to cross Wallace's line. Furthermore, we consider that the frequent change of sea levels during the Pleistocene propelled the diversification of sect. *Trigonostemon* in Borneo and the Malay Peninsula.

Additional key words

dated phylogeny
Dispersal-Extinction-Cladogenesis
Pleistocene
Quaternary
speciation
Statistical Dispersal-Vicariance analysis
Tritaxis
Wallace's line

INTRODUCTION

Southeast Asia ranges from the Alpine-Himalayan mountain belt south-eastwards to a massive collection of islands across the equator between 95°E and 140°E (Hall 2009), which is commonly known as the Malay Archipelago (Wallace 1869) or Malesia (Zollinger 1857, van Steenis 1948b, 1950, Raes & van Welzen 2009). The SE Asian mainland (Sundaland continental core) and W Malesia (Sunda Shelf) were already attached in the Mesozoic, while the much younger E Malesia was formed by continental fragments that mainly rifted from the Australian part of the splitting Gondwana since the Eocene (Hall 2009).

Malesia represents a rich biodiversity. This area harbours a total of approximately 42,000 plant species (Roos 1993), 70% of which is endemic (van Welzen 2005). Plant dispersals in this area have facilitated the floristic exchange between the continents of Asia and Australia (e.g., Sirichamorn et al. 2014, Crayn et al. 2015, Buerki et al. 2016, Hauenschild et al. 2018). The Malesian islands form a more or less linear pathway of stepping stones for plant dispersals (van Welzen et al. 2005). However, significant water barriers (e.g., Makassar Strait and Banda Sea) exist in Wallacea, the central part of Malesia (most of Java, Lesser Sunda Islands, Sulawesi, Philippines, Moluccas; van Welzen et al. 2011), and the stepping stones (e.g., Moluccas) only emerged above sea level since 10 Ma (Hall 2009). At present, the climate in Malesia is everwet in the west (Sunda Shelf: Malay Peninsula, Sumatra, Borneo, SW Java) and the east (Sahul Shelf: New Guinea); while in most parts of Wallacea, there is a yearly dry monsoon. Because climate (especially the yearly precipitation and temperature) is a very important regulator of species occurrences (Boucher-Lalonde et al. 2012, Araújo et al. 2013), it may have overruled the historical dispersal pathways. Relatively few studies attempted to reveal the exact migration route for plants across Wallace's line. The most often used route between east and west is via the Philippines (Nauheimer et al. 2012, Denduangboripant et al. 2001; or vice versa, e.g., Thomas et al. 2012, Jønsson et al. 2010 [bird]), but other routes are also found (e.g., via Borneo and Sulawesi, Grudinski et al. 2014, Thomas et al. 2012, Evans et al. 2003 [frog]; or between Java and the Lesser Sunda Islands (e.g., proposed route by Su & Saunders 2009, present in Figure 7; Chantarasuwan et al. 2016). General migration patterns can only be discovered when a sufficient number of case studies are performed. In this paper, we add an example of the historical biogeography of *Trigonostemon* Blume and *Dimorphocalyx* Thwaites, by investigating their geographical origin and dispersal routes, particularly those across Wallace's line, and comparing these to the previous studies.

Trigonostemon and *Dimorphocalyx* are two closely related genera in the Euphorbiaceae, comprising about 60 (Yu & van Welzen 2018) and 13 species (van Welzen & van Oostrum 2015), respectively. They are both classified in tribe Codiaeae (Pax) Hutch. of the subfamily Crontonoideae (Webster 2014) and are morphologically similar in the connate stamens and the presence of petals in both staminate and pistillate flowers. Both genera have more or less the same SE Asian distribution, ranging from India to S China, throughout continental SE Asia and Malesia to NE Australia, and for *Trigonostemon*, even to the W Pacific (Govaerts et al. 2000, van Welzen & van Oostrum 2015, Yu & van Welzen 2018).

The main differences between the two genera lie in the sexual system and the number and arrangement of the stamens: *Trigonostemon* species are monoecious shrubs or trees with only one whorl of 3 or 5 connate stamens, whereas most *Dimorphocalyx* species are dioecious trees and often have 10–15 stamens arranged in two or three whorls, of which only the inner whorls are partly connate. *Dimorphocalyx* (including *Tritaxis* Baill., the two genera will be merged as one under the name *Tritaxis*, see Yu et al. 2019b) was once treated as a

section of *Trigonostemon sensu lato* (Müller Argoviensis 1865, 1866, Beddome 1873), but our recent molecular phylogenetic study (Yu et al. 2019b) demonstrated that *Trigonostemon* and *Dimorphocalyx* were two separate monophyletic groups within the C2 clade of the Crotonoideae in the backbone phylogeny of the Euphorbiaceae (Wurdack et al. 2005). Therefore, they are treated as separate genera as in their original generic circumscriptions (Blume 1825; Thwaites 1861).

West Malesia is the distribution centre for *Trigonostemon*. Within the genus, sect. *Trigonostemon* contains most species (about 50% species of the genus), and these species are likely the result of a series of recent speciation events (which is reflected in the short branches in the phylogram; Yu et al. 2019b). Particular factors in the tectonic and climatological history of this region may have promoted these events. Therefore, another aim of this paper is to provide an explanation for the rapid diversification in sect. *Trigonostemon* from a historical biogeographic angle.

MATERIAL AND METHODS

Divergence time estimation

The same specimens and molecular markers as in Yu et al. (2019b) were used to estimate the divergence times of *Trigonostemon* and *Dimorphocalyx*. A total of 41 species (out of about 60) and 6 varieties of *Trigonostemon* and 11 species (out of about 13) of *Dimorphocalyx* were included. The sampling covers the whole distribution of the two genera, except *Trigonostemon* sect. *Pycnanthera* Benth. (*T*. *diplopetalus* Thwaites and *T*. *nemoralis* Thwaites from S India and Sri Lanka) is missing.

The molecular dating analysis was performed on matrix 1 of Yu et al. (2019b) using Bayesian Inference via BEAST v.1.10.1 (Suchard et al. 2018). Five molecular markers were used: the nuclear ITS and the chloroplast *trnK* intron, *trnT-L*, *trnL-F* and *rbcL*. In the data matrix, sequences of all these five markers obtained for *Trigonostemon* and *Dimorphocalyx* are aligned with the dataset of the Euphorbiaceae (based on *trnL-F* and *rbcL*) of Wurdack et al. (2005).

The substitution model of the nuclear and chloroplast markers was selected based on the lowest Akaike Information Criterion scores detected by Modeltest-NG v.0.1.5, which showed the same model for the nuclear and chloroplast markers. The input file was created by BEAUti v.1.10.1 (part of the BEAST package) with the following settings: the dataset contained five partitions (each partition for a single molecular marker); the substitution rates were calculated under the General Time Reversal (GTR) model with a discrete Gamma distribution (+Γ, 4 categories) of evolutionary rates among the sites and a certain number of invariable sites (+I); the divergence times were estimated using the uncorrelated relaxed clock model (Drummond et al. 2006) with a lognormal distribution of rates; the Yule process was selected as tree prior (Yule 1925; Gernhard 2008), and a random starting tree was used; a total of 1.25×10^8 generations of Markov Monte Carlo chains were performed and trees were sampled every 1×10^4 generations. The results were examined for Effective Sampling Size (ESS > 200) using Tracer v.1.7.1 (Rambaut et al. 2018). The first 20% of the sampled trees was discarded as burn-in, and the Maximum Clade Credibility (MCC) tree was found using TreeAnnotator v.1.7.5 (part of the BEAST package).

Three calibration points were used to estimate the divergence times. As no distribution type of the fossil ages was known, the calibration priors were coded as uniform distributions (Ho 2007)

with an upper and lower boundary (presented between brackets). Because no fossil records directly identified as *Trigonostemon* or *Dimorphocalyx* could be found, we used two secondary calibrations and a fossil record of *Hippomaneoidea warmanensis* Crepet & Daghlian instead:

1. The crown node of Euphorbiaceae s.s. (Figure 41; the node joining Acalyphoideae s.s. and Euphorbioideae) was assigned a mean age of 89.9 Ma (97.4–81.2 Ma). The age was taken from a phylogenomic study of the Malpighiales (Xi et al. 2012). In our phylogeny, this node refers to most of the taxa, only the Peroideae (Wurdack et al. 2005; presently the Peraceae), the Pandaceae and the outgroup, the Humiriaceae, are excluded.

2. The crown node of *Trewia nudiflora* L. (presently *Mallotus nudiflorus* (L.) Kulju & Welzen) and *Mallotus japonicus* (Spreng.) Müll.Arg. (see Figure 3 in Wurdack et al. 2005, within the A1 clade of the subfamily Acalyphoideae s.s. in Wurdack et al. 2005) was assigned a mean age of 34.31 Ma (44.79–32.35 Ma). This is the inferred age of the ancestral species of *Mallotus* (Figure 3, node 113, in van Welzen et al. 2014).

3. The crown node of Hippomanoids (equivalent to tribe Hippomaneae in Webster 2014; see Figure 3 in Wurdack et al. 2005, including both H1 and H2 clades of the subfamily Euphorbioideae) was assigned a mean age of 42.8 Ma (47.8–37.8 Ma). The data was obtained from a fossil collected from the Claiborne Formation of middle Eocene (Crepet & Daghlian 1982). The geological timescale of middle Eocene (Lutetian and Bartonian) was thus used to determine the upper and lower bounds, of which the average value was assigned as the mean age. The fossil was named *Hippomaneoidea warmanensis* Crepet & Daghlian. It was selected because it contained well-preserved inflorescences and pollen, and we consider the identification credible. The closest affinities of the fossil seemed to be the tribe Hippomaneae, as the floral and palynological characters are shared among several genera (from both H1 and H2 clades in Wurdack et al. 2005) in the tribe (Crepet & Daghlian 1982). Therefore, we assigned this calibration point to the ancestral taxon of the whole tribe.

Ancestral area reconstruction

A total of 15 areas (Figure 49; Table 6) were delimited based on the distribution of extant taxa, the tectonic history and the presence of endemic species. For example, Palawan (Figure 49, area I) was set apart from the rest of the Philippine islands (area J) due to its different geological origin (Hall 2002) and the presence of two endemic species (*Trigonostemon* sp. 2 and *T. victoriae* R.Y.Yu & Welzen); Northeast India (including Bangladesh and a small part of W Myanmar) is separate from SE Asian mainland because of two endemic species (*Trigonostemon* sp. 3, *T. semperflorens* (Roxb.) Müll.Arg.).

The MCC tree from the dated phylogeny was first modified, whereby the redundant taxa (mainly the species that are not part of *Trigonostemon* or *Dimorphocalyx*) were removed from the tree and only the same taxa (i.e., 41 species and 6 varieties of *Trigonostemon*, 12 species of *Dimorphocalyx*, *Tritaxis gaudichaudii* Baill., *Ostodes paniculata* Blume and *Jatropha gossypifolia* L.) as in matrix 2 in Yu et al. (2019b) remained. This modified MCC tree was used for the likelihood analyses (DEC) via the package RASP 4.0 (Reconstruct Ancestral State in Phylogenies; Yu et al. 2015). Prior dispersal constraints between the areas in four time frames (Table 7) were defined based on the geographical distances at the relevant time (Hall 2002, 2009). An extra Bayesian analysis was performed based on the matrix 2 (Yu et al. 2019b) via BEAST v. 1.10.1 under the same parameters as above (but without calibration points). The last obtained 10,000 trees were used as input in the S-DIVA analyses. A maximum

of 2–3 areas were optimised per node in the DEC analyses, and 2–4 in the S-DIVA analyses; higher numbers of area took much longer computation and often gave more ambiguous results (i.e., many possibilities, but each with a low probability and with often tectonically unlikely combinations of areas).

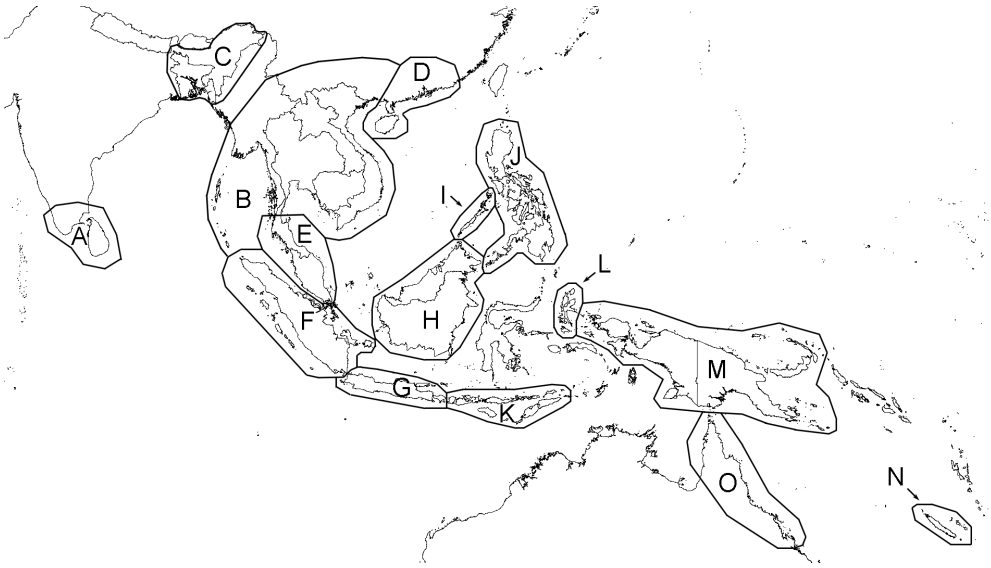

Figure 49 Area delimitation used for the historical biogeographic reconstruction of *Trigonostemon* and *Dimorphocalyx*: A. S India and Sri Lanka; B. SE Asian mainland including the Andaman and Nicobar Islands; C. NE India, Bangladesh and W Myanmar; D. S China (Guangdong and Hainan); E. S Peninsular Thailand and the Malay Peninsula; F. Sumatra; G. Java and Bali; H. Borneo; I. Palawan; J. the Philippine Islands excluding Palawan; K. Lesser Sunda Islands excluding Bali; L. N Moluccas; M. New Guinea; N. New Caledonia; O. NE Australia.

Table 6 Distribution of the sampled taxa. The authorities of the taxa are also shown in the table. The abbreviations in the column 'Distribution' refer to the areas discriminated in Figure 49. *Trigonostemon* sp. 1 will be described as *T. palustris* R.Y.Yu & Welzen (Yu et al. 2019a); *Trigonostemon* sp. 2 will be described as *T. montanus* R.Y.Yu & Welzen (2019b); we were unable to identify *Trigonostemon* sp. 3 for the time being.

Taxon	Distribution
Trigonostemon semperflorens (Roxb.) Müll.Arg.	C
Trigonostemon polyanthus Merr.	J
Trigonostemon villosus Hook.f. var. *borneensis* (Merr.) Airy Shaw	FHJ
Trigonostemon filiformis Quisumb.	HJ
Trigonostemon detritiferus R.I.Milne	H
Trigonostemon villosus Hook.f. var. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen	HIJ
Trigonostemon cf. *filiformis* Quisumb.	HJ
Trigonostemon villosus Hook.f.var. *cordatus* R.Y.Yu & Welzen	H
Trigonostemon lychnos (R.I.Milne) R.Y.Yu & Welzen	H
Trigonostemon villosus Hook.f. var. aff. *merrillianus* (Airy Shaw) R.Y.Yu & Welzen	HIJ
Trigonostemon verticillatus (Jack) Pax var. *verticillatus*	BE
Trigonostemon flavidus Gagnep.	BD

Table 6 (cont.)

Taxon	Distribution
Trigonostemon diffusus Merr.	H
Trigonostemon sp. 1	I
Trigonostemon victoriae R.Y.Yu & Welzen	I
Trigonostemon longipes (Merr.) Merr.	J
Trigonostemon malaccanus Müll.Arg.	BEF
Trigonostemon murtonii Craib	B
Trigonostemon beccarii Ridl.	F
Trigonostemon pentandrus Pax & K.Hoffm.	E
Trigonostemon verticillatus (Jack) Pax var. *salicifolius* (Ridl.) Whitmore	E
Trigonostemon rufescens Jabl.	E
Trigonostemon balgooyi R.Y.Yu & Welzen	E
Trigonostemon villosus Hook.f. var. *villosus*	E
Trigonostemon capillipes (Hook.f.) Airy Shaw	E
Trigonostemon magnificus R.I.Milne	F
Trigonostemon merrillii Elmer	IJ
Trigonostemon sandakanensis Jabl.	H
Trigonostemon longifolius Wall. ex Baill.	BCDEFHJ
Trigonostemon reidioides (Kurz) Craib	B
Trigonostemon viridissimus (Kurz) Airy Shaw var. *viridissimus*	BCDEFGHJK
Trigonostemon verrucosus J.J.Sm.	B
Trigonostemon quocensis Gagnep.	BCE
Trigonostemon laevigatus Müll.Arg. var. *laevigatus*	BEFGHIJ
Trigonostemon sp. 3	B
Trigonostemon albiflorus Airy Shaw	BD
Trigonostemon wui H.S.Kiu	BD
Trigonostemon sp. 2	C
Trigonostemon cherrieri J.M.Veillon	N
Trigonostemon inopinatus Airy Shaw	O
Trigonostemon aurantiacus (Kurz ex Teijsm. & Binn.) Boerl.	BEFG
Trigonostemon xyphophylloides (Croizat) L.K.Dai & T.L.Wu	D
Trigonostemon hartleyi Airy Shaw	M
Trigonostemon philippinensis Stapf	BEFHJ
Trigonostemon bonianus Gagnep.	B
Trigonostemon adenocalyx Gagnep.	B
Trigonostemon lii Y.T.Chang	B
Ostodes paniculata Blume	BDEFG
Dimorphocalyx moluccensis Welzen & Oostrum	L
Dimorphocalyx sp.	H

Table 6 (cont.)

Taxon	Distribution
Dimorphocalyx malayanus Hook.f.	EHJ
Dimorphocalyx glabellus Thwaites	A
Dimorphocalyx beddomei (Benth.) Airy Shaw	A
Tritaxis gaudichaudii Baill.	B
Dimorphocalyx ixoroides (C.B.Rob.) Airy Shaw	J
Dimorphocalyx trichocarpus (Airy Shaw) Welzen & Oostrum	H
Dimorphocalyx denticulatus Merr.	EFHIJ
Dimorphocalyx pauciflorus (Merr.) Airy Shaw	H
Dimorphocalyx muricatus (Hook.f.) Airy Shaw	EFH
Dimorphocalyx australiensis C.T.White	KMO
Dimorphocalyx cumingii (Müll.Arg.) Airy Shaw	J

RESULTS

Dated molecular phylogeny (Figure 50; Table 8)

The molecular dating analysis (Figure 50) results in a similar phylogeny as in Yu et al. (2019b). Compared to the results obtained via MrBayes (Figure 42), the MCC tree generated by BEAST is more similar to the results from the ML analyses (Figure 48): three species (*Trigonostemon adenocalyx* Gagnep., *T. bonianus* Gagnep. and *T. lii* Y.T.Chang; distributed in SW China and Indochina) are branching at the base in the T3 clade (in the BI analysis via MrBayes they were one node higher in the clade), and *T. magnificus* R.I.Milne (endemic to Sumatra) is at the base of sect. *Trigonostemon* (with MrBayes it is sister to *T. beccarii* Ridl., which is also an endemic species in Sumatra).

Trigonostemon is estimated to have diverged from other crotonoids with inaperturate pollen between 25.77 (95% highest posterior density interval [HPD]: 35.85–22.87) Ma and 18.8 (26.35–16.33) Ma. The ages of the crown group of sect. *Trigonostemon*, sect. *Spinipollen* and sect. *Tylosepalum* are 12.9 (16.05–8.22) Ma, 14.25 (18.93–8.27) Ma and 17.82 (24.06–14.65) Ma, respectively. The divergence times of the extant taxa in sect. *Trigonostemon* are often relatively younger than those in the other two sections. More than half of the extant taxa of sect. *Trigonostemon* are estimated to have probably diverged during the Pleistocene (i.e., lower bound of HPD younger than 2.58 Ma). The divergence of *Dimorphocalyx* from other inaperturate crotonoids is inferred between 29.04 (38.11–24.11) Ma and 23.72 (30.45–13.54) Ma.

Historical biogeography (Figure 51; Table 8)

The most probable ancestral area of *Trigonostemon* (node 108, Figures 50, 51) is inferred to be SE Asian mainland by both DEC (relative probability, RP = 1.0) and S-DIVA (marginal probability, MP = 0.97). Section *Tylosepalum* Pax & K.Hoffm. (crown node 107, Figures 50, 51) diverges first but still remains on the SE Asian mainland (RP = 1.0, MP = 1.0), where it further speciates. Some species then radiate or disperse east- and southwards, resulting in a wider distribution. Two long-distance dispersal events involve the crossing of Wallace's line (between nodes 99 and 98, and between nodes 103 and 102 [S-DIVA] or between node 102 and

Table 7 Prior dispersal constraints between the areas (A–O, see Figure 43) for DEC analysis. The dispersal constraints are estimated by the absolute distances (Hall 2009) between the relevant areas in the concerning time frames. Lower values indicate stronger constraints.

10 Ma–present

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
A		0.8	0.8	0.7	0.7	0.6	0.5	0.6	0.4	0.4	0.3	0.1	0.1	0.1	0.1
B	0.6		1	1	1	0.9	0.8	0.9	0.7	0.6	0.6	0.3	0.2	0.1	0.1
C	0.7	1		0.9	0.9	0.8	0.7	0.7	0.7	0.7	0.6	0.4	0.2	0.1	0.1
D	0.5	1	1		0.9	0.8	0.7	0.7	0.7	0.7	0.6	0.4	0.2	0.1	0.1
E	0.5	1	1	1		1	0.9	1	0.7	0.6	0.7	0.3	0.2	0.1	0.1
F	0.4	0.7	0.6	0.6	0.8		1	0.9	0.7	0.6	0.8	0.4	0.3	0.1	0.1
G	0.2	0.5	0.4	0.4	0.6	0.8		0.9	0.6	0.6	0.9	0.5	0.4	0.2	0.2
H	0.5	0.9	0.8	0.8	1	0.8	0.8		0.9	0.9	0.7	0.6	0.4	0.2	0.2
I	0.3	0.7	0.7	0.7	0.7	0.6	0.5	0.8		0.9	0.5	0.4	0.2	0.1	0.1
J	0.3	0.5	0.6	0.6	0.6	0.6	0.6	0.9	0.9		0.6	0.6	0.5	0.3	0.3
K	0.1	0.3	0.3	0.3	0.4	0.4	0.8	0.5	0.4	0.4		0.6	0.6	0.4	0.4
L	0.1	0.2	0.2	0.2	0.3	0.3	0.4	0.4	0.3	0.3	0.4		0.9	0.7	0.7
M	0.1	0.2	0.2	0.2	0.2	0.2	0.4	0.4	0.3	0.3	0.5	0.9		0.8	0.7
N	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.3	0.7	0.8		0.7
O	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.3	0.7	0.7	0.7	

20–10 Ma

30–20 Ma

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
A		0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0	0	0	0	0
B	0		1	1	1	1	0.8	0.9	0.7	0.6	0.1	0.1	0.1	0.1	0.1
C	0	1		1	1	1	0.7	0.8	0.8	0.5	0.1	0.1	0.1	0.1	0.1
D	0	1	1		1	1	0.7	0.8	0.8	0.5	0.1	0.1	0.1	0.1	0.1
E	0	1	1	1		1	0.8	1	0.7	0.6	0.1	0.1	0.1	0.1	0.1
F	0	1	1	1	1		1	0.9	0.6	0.7	0.1	0.1	0.1	0.1	0.1
G	0	0.9	0.8	0.8	1	1		0.9	0.5	0.7	0.3	0.1	0.1	0.1	0.1
H	0	1	1	1	0.9	1	1		0.7	0.9	0.1	0.2	0.2	0.1	0.1
I	0	0.7	0.8	0.8	1	1	0.5	0.6		0.8	0.1	0.1	0.1	0.1	0.1
J	0	0.5	0.4	0.4	0.6	0.5	0.7	0.8	0.5		0.1	0.2	0.2	0.1	0.1
K	0	0	0	0	0.5	0.6	0.2	0.1	0	0		0.2	0.2	0.1	0.1
L	0	0	0	0	0	0	0.1	0.1	0	0	0.1		0.8	0.6	0.6
M	0	0	0	0	0	0	0	0	0	0	0	0.1		0.9	0.7
N	0	0	0	0	0	0	0	0	0	0	0	0	1		0.7
O	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0.7	

54–30 Ma

Table 8 Summary of the dated phylogeny and ancestral areas. Shown from left to right are node numbers, posterior probabilities, mean ages of the nodes, 95% Height of the Posterior Density intervals, DEC reconstructions and relative probability, S-DIVA reconstructions and marginal probability and remarks. In either analysis, only the optimization with the highest probability is shown. When the analyses result in different reconstructions with different maximum numbers of areas, the extra results are indicated in the remarks. The abbreviations (A–O) indicate the areas shown in Figure 43. The cross icon '†' refers to many possibilities.

Node	Posterior	Age	95% HPD	DEC	RP	S-DIVA	MP	Remarks
63	0.71	1.42	3.68–0.8	H	0.76	H	0.96	
64	0.38	0.52	1.78–0.09	H	0.85	H	1	
65	0.94	0.82	2.63–0.28	H	1	H	1	
66	0.18	1.53	4.21–1.11	H	1	H	1	
67	0.14	1.72	4.81–1.66	H	0.82	H	1	
68	1	0.81	2.5–0.11	H	1	H	1	DEC 3: HIJ=0.52
69	0.52	1.83	5.4–1.9	H	0.62	H	0.98	DEC 3: HJ=0.52
70	0.5	4.27	5.67–2.07	J	0.55	H	0.85	DEC 2: HJ=0.41
71	0.31	5.81	7.97–2.84	H	0.18	CH	0.82	DEC 3: CJ=0.16
72	0.98	2.94	6.1–1.62	B	0.6	B	1	
73	0.48	5.61	7.55–2.94	BH	0.46	BH	0.99	
74	0.17	8.85	8.59–4.2	B	0.62	BH	0.56	
75	1	2.71	4.19–0.94	I	1	I	1	
76	1	3.96	5.9–1.98	IJ	0.62	IJ	0.9	
77	0.16	7.67	7.59–3.05	B	0.54	BI	0.47	S-DIVA 3: BEI=BI=BFI=0.14; 4: BEI=BI=BFI=BEFI=0.09
78	0.78	9.11	8.03–3.36	B	0.88	BI	0.39	
79	0.52	9.23	9.98–5.17	B	0.52	B	0.28	
80	0.94	2.28	2.68–0.37	E	1	E	1	
81	1	3.25	3.82–0.82	E	1	E	1	
82	1	4.43	6.36–1.99	EF	0.59	EF	1	
83	0.66	5.63	6.91–1.8	E	1	E	1	
84	0.67	7.71	8.47–3.34	E	0.87	E	1	
85	0.27	10.38	11.83–6.44	BE	0.47	BE	0.4	
86	1	11.06	12.66–6.81	BE	0.46	BE	0.66	
87	1	12.9	16.05–8.22	BE	0.33	BF	0.66	DEC 3: B=0.25; S-DIVA 3: BEF=BF=0.25; S-DIVA 4: BEF=BF=0.18
88	1	3.46	8.75–1.95	H	1	BH=H=HJ	0.33	S-DIVA 3: †=0.08 all with H; 4: unable to calculate
89	1	6.46	11.91–3.75	HI	0.23	HJ	0.2	S-DIVA 3: †=0.06; 4: unable to calculate
90	1	14.25	18.93–8.27	B	0.72	BH=B =BJ=BI	0.25	S-DIVA 3: †=0.14 all with B; 4: † all with B
91	0.96	18.02	23.96–13.73	B	1	B	0.57	
92	0.95	7.84	11.93–4.78	B	1	B	1	
93	1	4.4	10.3–2.97	B	0.76	B	1	
94	1	10.87	13.8–6.48	B	1	B	1	

Table 8 (cont.)

Node	Posterior	Age	95% HPD	DEC	RP	S-DIVA	MP	Remarks
95	1	0.84	3.02–0.09	BD	0.83	B	1	
96	1	5.95	11.93–3.79	BC	0.43	BC	1	DEC 2: B=0.44
97	0.52	9.91	14.31–6.43	B	1	B	1	
98	0.99	8.42	11.8–3.17	O	0.28	NO	1	
99	0.98	10.56	16.28–8.56	B	0.37	B	0.69	
100	1	13.46	18.42–10.66	B	1	B	1	
101	1	7.35	11.33–2.97	D	0.58	BD	1	S-DIVA 3: BDE=BDG=BD=BDF=0.25; 4: † 0.14 all with BD
102	0.99	10.87	15.22–5.96	B	0.46	BM	1	DEC 3: M=0.42; S-DIVA 3: †=0.2, all with BM, 4: †=0.09, all with BM
103	1	12.31	17.93–9.23	B	0.43	B	1	
104	1	16.75	21.14–12.92	B	1	B	1	
105	1	2.14	1.93–0.04	B	1	B	1	
106	1	5.06	6.9–1.15	B	1	B	1	
107	0.99	17.82	24.06–14.65	B	1	B	1	
108	1	18.8	26.35–16.33	B	1	B	0.97	Divergence of *Trigonostemon*
109	1	25.77	35.85–22.87	B	1	B	0.96	
110	0.96	3.35	6.22–0.03	HL	0.82	HL	1	
111	1	0.23	1.55–0	A	1	A	1	
112	0.96	2.78	8.27–2.36	A	0.56	AH	0.99	DEC 3: AEH=0.34; S-DIVA 3: AH=AEH=AHJ=0.33; 4: AH=AHJ=AEH=AEHJ=0.25
113	0.86	6.01	10.02–3.65	H	0.62	BH	0.99	S-DIVA 3: ABH=BHJ=BH=BEH=0.25; 4: †=0.14 all with BH
114	0.86	5.19	5.19–0.99	H	1	H	0.99	
115	0.97	6.36	6.89–1.75	H	0.8	HJ	0.92	
116	0.88	6.97	11.19–4.61	H	0.71	H	0.9	
117	1	10.02	13.66–5.58	H	1	H	0.98	
118	1	1.75	8.9–0.92	H	1	H	1	DEC 3: EFH=0.59
119	1	10.69	20.06–8.49	H	0.84	H	0.99	
120	1	12.78	14.43–2.74	J	0.5	JM=JO=JK	0.33	S-DIVA 3: †=0.17 all with J; 4: †=0.14 all with J
121	0.99	23.72	30.45–13.54	H	0.38	HM=HO =HK=HJ	0.25	Divergence of *Dimorphocalyx*; S-DIVA 3: †=0.1 all with H; 4: †=0.07 all with H

T. *hartleyi* Airy Shaw [DEC], Figures 50, 51), but it is unclear via which route these dispersals happened. The DEC analysis (3 maximum areas) also indicates a westward dispersal event from New Guinea to west Malesia (from node 102 to *T*. *philippinensis* Stapf, Figures 50, 51), but in the S-DIVA analysis, it is more likely a vicariance event. Section *Spinipollen* R.Y.Yu & Welzen diverges on the SE Asian mainland (node 90, Figures 50, 51, RP = 0.72, four possibilities in S-DIVA, but all contain SE Asian mainland) and dispersed to Borneo and the Philippines

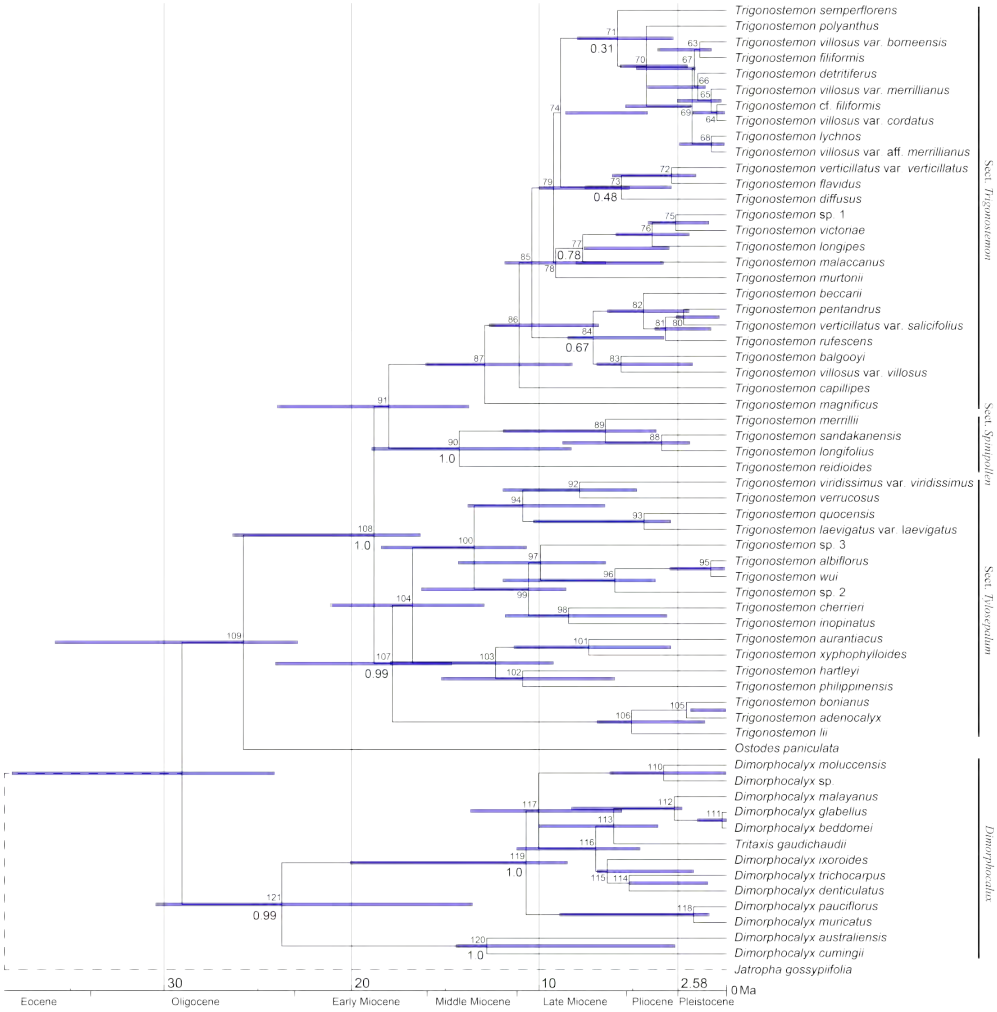

Figure 50 Chronogram (MCC tree) of *Trigonostemon* and *Dimorphocalyx* generated by a dated Bayesian analysis via BEAST. The redundant taxa in the analysis were removed. The posterior probabilities of important nodes are shown below the relevant branches. The blue node bars indicate the 95% Height of the Posterior Density interval (HPD). Dash lines mean the branch length has been modified.

(either Palawan or the Philippine islands, but both with low support; node 89, Figures 50, 51, RP = 0.23, MP = 0.2). A possible vicariance event follows, leading to the split of *T*. *merrillii* Elmer and the ancestral species of *T*. *longifolius* Wall. ex Baill. and *T*. *sandakanensis* Jabl.

Section *Trigonostemon* radiates to the Malay Peninsula (node 87, Figures 50, 51, RP = 0.33) or Sumatra (node 87, MP = 0.66; but this is less likely because node 87 represents a major difference in the results between BEAST and MrBayes, see above; the Malay Peninsula would be the only optimised area if the analyses were based on phylograms obtained using MrBayes and not BEAST, not shown). After *T*. *magnificus* and *T*. *capillipes* (Hook.f.) Airy Shaw have split off, the crown group remains on the SE Asian mainland and the Malay Peninsula (node 85, Figures 50, 51, RP = 0.47, MP = 0.4). After a vicaricance event, a lineage (crown node 84,

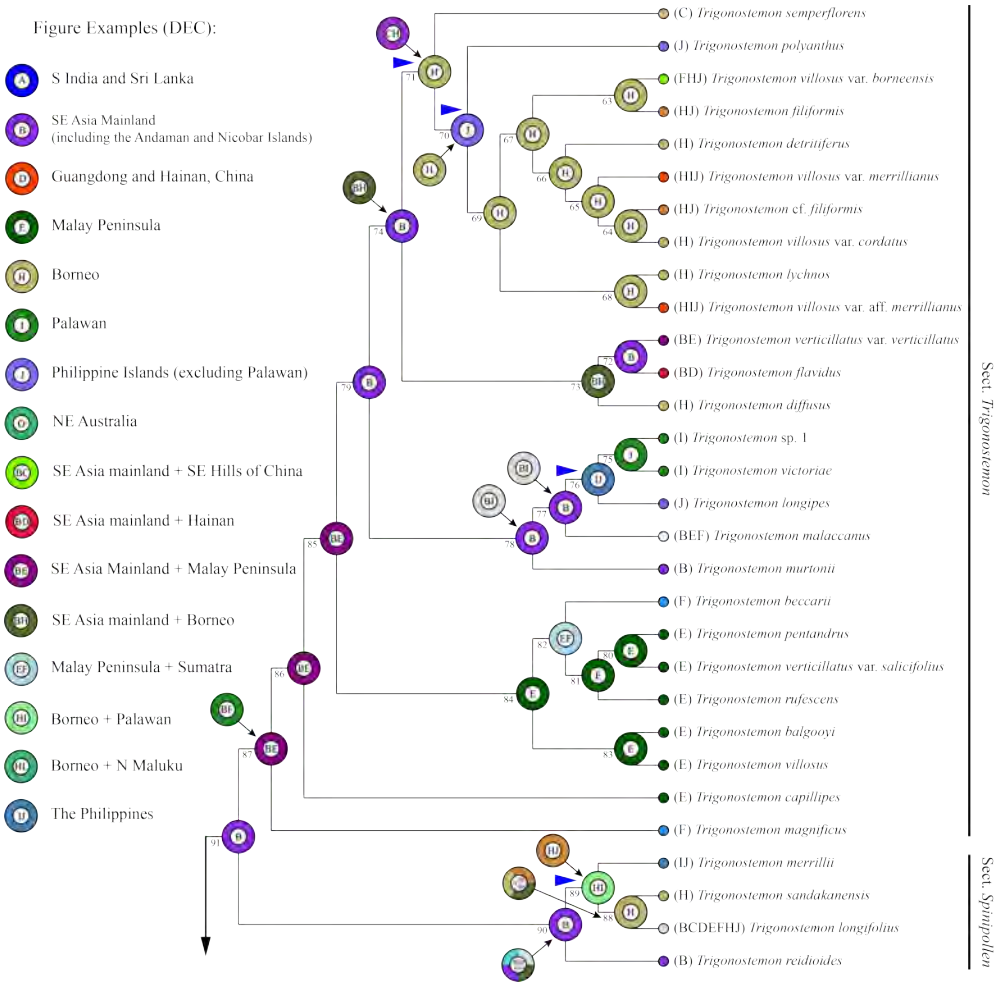

Figure 51 Ancestral area reconstructions of *Trigonostemon* and *Dimorphocalyx*. Distributions of taxa are shown at the end of the branches (see legend of Figure 43 for abbreviations). Only optimizations with the highest probability are shown in the figure (if the optimizations are different in analyses with different numbers of maximum areas). Results from the DEC analyses are shown at each node; when S-DIVA analyses yield a different optimization, the results are shown next to the relevant nodes. Blue arrows refer to dispersals from west to east; red arrows refer to dispersals from east to west.

Figures 50, 51, RP = 0.87, MP = 1.0) diverges and diversifies on the Malay Peninsula; the other lineage (three clades can be recognised) disperse (probably through Palawan, node 77, Figures 50, 51, MP = 0.47) to the Philippines and to Borneo. Rapid speciation events in this section are inferred to have occurred on the Malay Peninsula and Borneo (i.e., nodes 63–70 and 80–84, Figures 50, 51). It should be noted the posterior probabilities within sect. *Trigonostemon* (nodes 63–86, Figures 50, 51) are relatively low, the ancestral area reconstructions may be less definite (discussed below).

Borneo is inferred to be the most probable ancestral area of *Dimorphocalyx* (node 121, Figures 50, 51, RP = 0.38, four possibilities in S-DIVA, but all contain Borneo). A lineage disperses

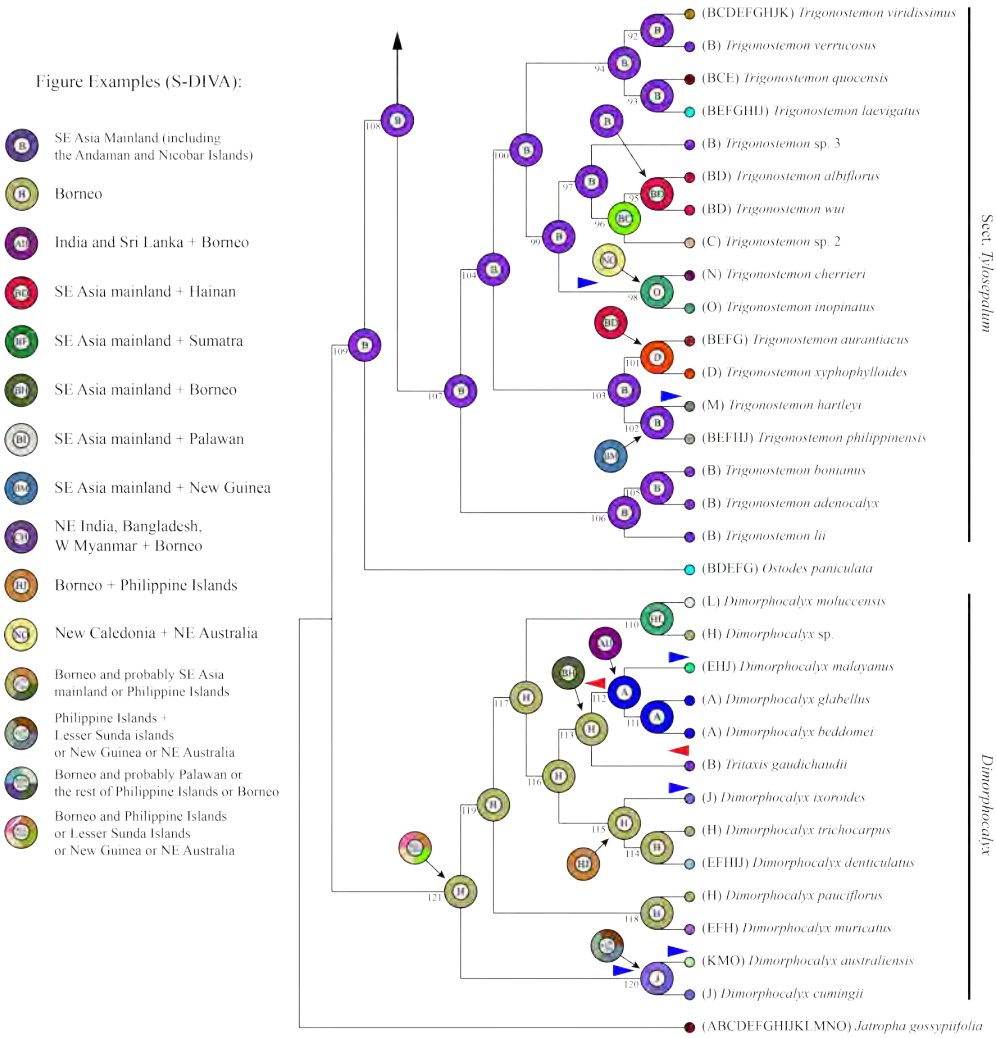

Figure 51 (cont.)

(node 121 to 120, Figures 50, 51) to first the Philippine islands (node 120, Figures 50, 51, RP = 0.5, three possibilities in S-DIVA, but all contains the Philippine islands; node age 12.78 [14.43–2.74] Ma) and then to E Malesia and NE Australia (*D. australiensis* C.T.White). The other lineage remains on Borneo and diversifies. The ancestral species of *Dimorphocalyx* sp. and *D. moluccensis* Welzen & Oostrum (node 110, Figures 50, 51) reached the north Moluccan islands through radiation at 10.02–3.35 Ma, and this was followed by a vicariance event, giving rise to these two species. Around 6.01–2.78 Ma, a lineage dispersed to S India (including Sri Lanka) probably through the SE Asian mainland (discussed below). Other modern *Dimorphocalyx* species are the result of radiations or dispersals in various directions from Borneo after 7 Ma.

DISCUSSION

Tree compatibility

The condensed (MCC) tree and the 10,000 background trees used in the DEC and S-DIVA analyses are generated based on two different data matrices. Because direct fossil records are lacking, the estimation of the divergence times in *Trigonostemon* and *Dimorphocalyx* was realised with the help of other Euphorbiaceae taxa. We therefore used a combined dataset (matrix 1 of Yu et al. 2019b), in which our molecular data of *Trigonostemon* and *Dimorphocalyx* are embedded into the dataset of the Euphorbiaceae (Wurdack et al. 2005), for a dated phylogenetic analysis (see Material and methods). Taxa irrelevant to the analysis of *Trigonostemon* and *Dimorphocalyx* were then removed from the MCC tree, and only the same taxa as in matrix 2 (Yu et al. 2019b) remained. The background trees for the S-DIVA analysis, however, are based on our molecular data only (i.e., matrix 2 of Yu et al. 2019b).

The MCC tree (Figure 50) and the background trees have the same topology for the main clades, and the ancestral areas reconstructed by the DEC and S-DIVA methods are highly similar. Matrix 1 includes 8 extra *rbcL* sequences compared with matrix 2, but the marker contains very little variation within *Trigonostemon* (Yu et al. 2019b); it only helps to determine the phylogenetic position of *Trigonostemon* in the Euphorbiaceae, but it has almost no impact on the internal relationships within the genus. Therefore, it is reasonable to display the probabilities calculated based on the 10,000 background trees in the S-DIVA analysis on the MCC tree. Using this strategy, we also avoided an unnecessary secondary Bayesian clock analysis. The divergence times were already inferred by indirect calibration points, a secondary dating phylogeny would have caused more bias.

Because of the missing data (Table 5) and high speciation rates (discussed below) of the taxa within sect. *Trigonostemon* (i.e., nodes 63–87, Figures 50, 51), several nodes have a relatively low (< 0.9) posterior probability in the dated molecular phylogeny. This may affect the credibility of the ancestral area reconstructions of these clades. However, the four main lineages (i.e., crown nodes 71, 73, 78, 84, Figures 50, 51) appeared relatively stable in the phylogenies reconstructed by different methods (MP, ML and BI, see Figures 42, 47, 48); the taxa more or less remained in the same lineage although the position might slightly change within the lineages. Moreover, most area reconstructions within these three lineages have high relative and marginal probabilities; thus they are still considered credible. In addition, the phylogenetic relationships of *Trigonostemon*, *Dimorphocalyx* and other genera in the C2 clade of crotonoids are still unsolved (Figure 41). *Jatropha* L. was used as the outgroup and was assigned a distribution of all areas. This may have made the reconstructions of the crown nodes (ancestral areas) of *Trigonostemon* and *Dimorphocalyx* less realistic, but the analyses gave strong signals for both crown nodes (for *Trigonostemon*, node 108, RP = 1.0, MP = 0.97; for *Dimorphocalyx*, node 121, RP = 0.38, four possibilities in S-DIVA, all contain Borneo, total MP = 1.0), which were reconstructed based on the internal taxa. Therefore, these reconstructions can be trusted.

Migration routes

Trigonostemon is inferred to have originated on the geologically old SE Asian mainland (it has formed a promontory of the Eurasian continent since the Early Mesozoic, Hall 2009). Historical migrations mainly occurred in sect. *Trigonostemon*: 1. radiating to the adjacent Malay Peninsula at around 18.02–12.9 Ma (node 91 to 87; then to 85, Figures 50, 51) and

2. eastward migrations from SE Asian mainland to Borneo (occurred in two linages: 1. from node 79 to 74 [S-DIVA] or from node 74 to 71 [DEC]; 2. from node 74 to 73) and to the Philippines (occurred in one lineage, possibly through Palawan: from node 79 to 78 [S-DIVA] or from node 77 to 76 [DEC]) around 9.23–3.96 Ma (Figures 50, 51). The former is easy to explain: the Malay Peninsula has always been connected to SE Asia and the permanent everwet climate in this part, also during the Pleistocene, has surely worked to the advantage of the plants (11 extant species in the Malay Peninsula; Yu & van Welzen 2018). This also appears to be a commonly used route (vs. a less common route through Taiwan to the Philippines, e.g., Matuszak et al. 2015; Condamine et al. 2013 [butterfly]) for plants of Asian origin to colonize parts of Malesia (e.g., Thomas et al. 2012, Denduangboripant et al. 2001, Ridder-Numan 1998; or the other way round, e.g., Haegens 2000, Grudinski et al. 2014). In the latter case, the radiation to Borneo was possible as the land was connected to the Malay Peninsula before at least 5 Ma (Hall 2009), and a similar scenario has also been recorded (e.g., Su & Saunders 2009); the dispersal (or radiation) via Palawan appears to be a new route: Palawan may have been a stepping stone for the dispersal (node 78 in S-DIVA), but no collection data is available for the islands to the west (e.g., the Spratly Islands); alternatively, Palawan, as the only microplate that moved from Asia to the east (starting ca. 30 Ma), may also have acted as an Ark of Noah, transporting *Trigonostemon* ancestral species to the Philippines. The results also indicate a possible dispersal from the SE Asian mainland to Borneo and the Philippines in sect. *Spinipollen* around 14.25–6.46 Ma (from node 90 to 89, Figures 50, 51), but no concrete conclusions can be made, because the support values for node 89 are low (RP = 0.23, MP = 0.2).

Dimorphocalyx probably originated around 29.04–23.72 Ma on Borneo. This was followed by the dispersal of one lineage from Borneo to the Philippines (node 121 to 120, Figures 50, 51) around 23.72–12.78 Ma. Similar dispersals have been recorded in several case studies (e.g., Nauheimer et al. 2012, Thomas et al. 2012, Su & Saunders 2009, Sheldon et al. 2012 [bird]), but these mostly occurred less than 12 Ma. Our results indicate that the exchange was already possible in an earlier time, probably up to Early Miocene, when the Sulu Archipelago and Tawi-Tawi islands had already been in place (Hall 2009). The dispersal from Borneo to S India and Sri Lanka (node 113 to 112, Figures 50, 51) at 6.01–2.78 Ma is somewhat difficult to explain: it is less likely that the plant dispersed (e.g., via birds) directly from W Malesia to S India, because the geographical distance is too long, but at that time the Indian plate had partly collided with SE Asian mainland (Patriat & Achache 1984), and long-distance dispersals between Borneo and S India/Sri Lanka (via land, wind, water or birds etc.) were indeed possible (e.g., Repetur et al. 1997; Sumatra was then mainly below water and had no impact on the dispersal; Hall 2009). Long distance dispersal may sound like an erratic occurrence, but the shape and size of India prior to its collision with Southeast Asia are unknown; north India may have been broad and big, thus greatly reducing the distance with Borneo. Alternatively, Southeast Asian mainland may have played a role, as before the plants reached S India (i.e., one node higher, at node 113, Figures 50, 51) an endemic species in Vietnam (*Tritaxis gaudichaudii* Baill.) diverged, and the S-DIVA analyses indicate a combination of Borneo + SE Asian mainland for node 113. Secondly, although the largest part of India always had a long dry season (Singhvi & Krishnan 2014), the coastal areas could have been wetter. Therefore, a possible dispersal route is via first SE Asian mainland (comparable hypotheses see e.g., Denduangboripant et al. 2001, Haegens 2000) and then NE India and E coastal India, where the plants may have become extinct later during dryer periods (distribution over land during wetter periods is also used to explain disjunct distributions between Africa and Asia, e.g., Chantarasuwan et al. 2016). If the missing sect. *Pycnanthera* (including two species from S India and Sri Lanka) had been included in the analyses, it would probably have revealed a migration route between

W Malesia and S India (but the optimizations of the crown group of *Trigonostemon* would not change because the signal is very strong; see above).

About half of the extant *Dimorphocalyx* species reached their current location through dispersal (i.e., from node 113 to *Tritaxis gaudichaudii* and from node 115 to *D. ixoroides* (C.B.Rob.) Airy Shaw, Figures 50, 51) or radiation (i.e., from node 114 to *D. denticulatus* Merr. and from node 118 to *D. muricatus* (Hook.f.) Airy Shaw, Figures 50, 51) since the Late Miocene (6.97–0 Ma). In that period, Borneo and the SE Asian mainland were still connected (Hall 2009) and stepping stones from Borneo to the Philippine Islands were already present (see above). If these events occurred during the Pleistocene when Sundaland was a connected landmass (Morley and Flenley 1987), radiation was even more probable (e.g., from node 118 to *D. muricatus*, Figures 50, 51).

Wallace's line

Wallace's line (1860) divides the floristic region of the Malay Archipelago into two parts (van Steenis 1950). The tectonic and climatic history of this region has caused different floras between W and E Malesia (van Welzen et al. 2005). Wallacea, a good phytogeographic region (about one third of the species are endemic), is also a transition zone between W and E Malesia (van Welzen et al. 2011) and plays an important role in the floristic exchanges (van Welzen et al. 2005).

The probably most often used migration route across the Wallace's line is through the Philippines to E Wallacea/New Guinea (Nauheimer et al. 2012, Denduangboripant et al. 2001; or vice versa, e.g., Thomas et al. 2012, Su & Saunders 2009, Jønsson et al. 2010 [bird]). The dispersal of the E Malesian species *D. australiensis* (node 121 to 120 then to E Malesia, Figures 50, 51) adds to these examples. Node 120 had an optimization of the Philippine islands in the DEC analysis. The other analyses yielded equal (S-DIVA) optimizations, but all of them contained the Philippine islands. Node 120 is the first divergence in *Dimorphocalyx*. It is inferred at an age (12.78 Ma) when the stepping stones in Wallacea were already in place (Hall 2009).

The other three dispersal events across Wallace's line do not show clear routes in the analyses. The most likely dispersal route for *D. moluccensis* (node 117 to 110, Figures 50, 51; divergence time 10.02–3.35 Ma) is also via the Philippines. On the one hand its sister species *Dimorphocalyx* sp. is endemic (?) to Sandakan (NE Borneo), which is close to the Philippines and the Sulu Archipelago and Tawi-Tawi islands could acted as stepping stones; on the other hand the Makassar Strait was always present and had a very strong current (Hall 2009). There is no record for *Dimorphocalyx* on Sulawesi, thus dispersal via Sulawesi seems unlikely. In *Trigonostemon*, the inferred ages of the two dispersal events (10.56–8.42 Ma between nodes 99 and 98, Figures 50, 51, 12.31–10.87 Ma between nodes 103 and 102, Figures 50, 51) are already possible for exchanges across Wallace's line (e.g., van Welzen et al. 2014). A possible westward dispersal is inferred after 10.87 Ma (node 102 to *T. philippinensis*, Figures 50, 51). Westward dispersals across the Wallace's line are less frequent (Richardson et al. 2012, Crayn et al. 2015) and often occurred after 8 Ma (Thomas et al. 2012, Su & Saunders 2009), but our results indicate that this could occur even earlier.

Rapid diversification

Section *Trigonostemon* experienced fast diversification in W Malesia during the Pleistocene, especially in two lineages, one on the Malay Peninsula (crown node 84, Figures 50, 51) and one on Borneo (crown node 71, Figures 50, 51). More than 2/3 of the taxa (19 out of 26) likely had their last speciation event in less than 2.58 Ma (Figure 50), which is hardly the case in the other two sections (their diversification mainly occurred in SE Asian mainland). *Trigonostemon* species are mostly small trees growing in lowland everwet forests characterised by Dipterocarp trees (Whitmore 1984) along rivers or coast lines (Yu & van Welzen 2018). These habitats (Heaney 1991) are to a great extent prone to the rise and fall of sea levels (repeated ca 50 times in the last 2.7 Ma, even up to -120 m during the last glacial maximum, Woodruff 2010): a fast expansion of the populations during the Pleistocene when sea levels were lower, after which the populations retreated to the islands and became isolated when the vast Sundaland broke up into fragments during interglacials, and consequently speciation events driven by vicariance occurred (Rand 1948).

The next question is why the rapid speciation events almost only took place on the Malay Peninsula and Borneo but not in SE Asian mainland or elsewhere? West Malesia was a connected landmass (Sundaland) during many Quaternary glacial maxima (Morley and Flenley 1987). This area is inferred to have been covered by Dipterocarp forests, particularly between S Malaya and Borneo (based on species distribution modelling for the LGM via the CCSM4 model; Raes et al. 2014). *Trigonostemon*, a typical rainforest group (Yu & van Welzen 2018), is also likely to have had the highest species richness in this area. After the Pleistocene, probably a great proportion of species became extinct as most of Sundaland submerged, the surviving ones remained on the Malay Peninsula in the west and Borneo in the east. The distribution of the extant species also corroborates this: the Malay Peninsula, N Borneo (Sarawak, Sabah and Brunei) and part of E Kalimantan (also with high postulated Dipterocarp forest density; Raes et al. 2014) represent most of the diversity in the genus (Yu & van Welzen 2018). As *Trigonostemon* and *Dimorphocalyx* mainly grow in everwet surroundings, diversification on the SE Mainland was likely reduced by climate, as the more northern from the equator, the more pronounced (longer and drier) the dry seasons.

CONCLUSIONS

The dated phylogeny enables us to interpret the historical biogeography of the morphologically similar genera *Trigonostemon* and *Dimorphocalyx* in the light of SE Asian tectonic history. Both genera are estimated to have diverged during the Oligocene, however, in probably different geographical locations: SE Asian mainland for *Trigonostemon* and Borneo for *Dimorphocalyx*. Compared to the hypothesised tectonic history of Malesia, all long-distance dispersals appear to have taken place when the stepping stones were in place. Most dispersal routes are supported by previous studies. The Philippines is inferred to have been the stepping stone for one of the more important dispersal routes across Wallace's line.

Similarly, the historical biogeography also allows us to further interpret the molecular phylogeny. The frequent change of the sea levels during the Pleistocene is considered to have facilitated the diversification in sect. *Trigonostemon*; and this is supported by the likely distribution of historical Dipterocarp forests in central Sundaland (Raes et al. 2014) and the extant *Trigonostemon* species. As a result, after leaving SE Asian mainland, one lineage of *Trigonostemon* succeeded to radiate or disperse to the Malay Peninsula and Borneo where it could diversify. In contrast, *Dimorphocalyx* mainly remained in its area of origin, Borneo, which is a possible reason why it diverged earlier than *Trigonostemon* but has fewer species.

Acknowledgments

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Chapter 8 Discussion and Conclusions

A monograph of the tropical Asian plant genus *Trigonostemon* Blume is presented. Taxonomic revisions are made according to the 'morphological species concept' based on herbarium and living material (Chapter 2–4). The species circumscriptions and recognition have been optimised. The more than 140 species described in the historical literature have now been reduced to 59 accepted species (including 3 uncertain species). The species complexes (i.e., *T*. *longifolius* Wall. ex Baill., *T*. *villosus* Hook.f. and *T*. *viridissimus* (Kurz) Airy Shaw) in the genus are now clearly outlined and reduced to single, variable species that can be recognised by morphological characters.

Species delimitation is a course of reasoning. By investigating a limited number of specimens, one has to decide what is part of the normal variability within a species and which are the specific discontinuities. *Trigonostemon* displays limited variation in the floral structures, but has highly variable vegetative characters. This was the problem in the species complexes, where (many) entities were discriminated based on variable characters. As soon as more material became available, it appeared that the variation was continuous and no species could be discriminated (e.g., obvious characters like the leaf shape and length of petiole, sometimes used as delimiting characters, can be highly variable within a species). Generally, the more inconspicuous characters (e.g., the number of stamens is a species indicative character) are often very useful to circumscribe the species complexes. The more variable species might be more common than usually expected, as they are often the 'result' of higher collecting densities, because 'the general (logical) experience is that increase of specimens brings along increase of variability, hence of the necessity of wider specific delimitation' (after van Steenis 1957). This is a drawback in making revisions. This means that the revision presented in this dissertation will not be the last and final conclusion. More molecular studies may reveal cryptic species within the present species delimitations.

An exploration of the pollen morphology of *Trigonostemon* and its close relatives is made using light and electron microscopy (Chapter 5). Two major types of pollen are found and correlate well with the macromorphology. Species with the *Trigonostemon reidioides* type pollen ('croton pattern' ornamentation) have deeply divided stigmas and a protruding appendage on the connective; species with the *Trigonostemon verrucosus* type pollen (verrucate exine) have slightly (or not) bifid stigmas and a connective without an appendage. Dimorphic pollen within a genus is possible, but it often occurs in different sections (Erdtman 1952). *Trigonostemon* pollen adds a good example. The correlations between pollen and macromorphology support the infrageneric classification of the genus (see below, also Chapter 6).

Molecular phylogenetic studies are made of *Trigonostemon*, *Dimorphocalyx* Thwaites and other closely related or morphologically similar taxa (Chapter 6). Five markers are used: the nuclear ITS and chloroplast *trnK* intron, *trnT-L*, *trnL-F* and *rbcL*. The generic circumscription of *Trigonostemon* has been solved. *Trigonostemon* and *Dimorphocalyx* are found to be two separate monophyletic groups within the inaperturate crotonoids. Because they are not sister groups, they are treated as separate genera. An infrageneric classification of *Trigonostemon* is proposed. Three monophyletic sections are supported based on the molecular phylogeny; one section, not included in the phylogeny, is treated based on its exceptional morphology and limited distribution. The main characters used to define the sections (the selection of these characters is discussed below) are the division of stigmas, the presence of a protruding appendage on the connective, the disc shape and the exine sculpture of the pollen grains. In addition, *Dimorphocalyx* and *Tritaxis* are phylogenetically and morphologically congeneric, and are merged under the latter genus name.

In phylogenetic systematics, 'a monophyletic group can only be confirmed by demonstrating their common possession of derivative characters (synapomorphies)' (after Hennig 1965). When the pollen characters are mapped on the molecular phylogeny, it has become clear that the verrucate pollen is such a derived character shared in clade T3 (Figure 42), and thus supports sect. *Tylosepalum* (Kurz) Benth; while the 'croton pattern' ornamentation is a shared primitive character state (symplesiomorphy) among all major clades in *Trigonostemon*. This is a phylogenetic interpretation of the pollen morphology.

Furthermore, the molecular phylogeny proves to be a powerful tool in the (infra)generic (and higher ranks) classification. Morphological characters of *Trigonostemon* show a high degree of variability (discussed above, also in Chapter 2) or homoplasy (e.g., although the number of stamens is a good indicator for species, but it seems to be 'randomly distributed' among the species when mapped on the phylogeny and shows a high amount of homoplasy, see Figure 42). The combination of a molecular phylogeny and the morphological characters mapped on it works well to find the synapomorphies by which the sections are recognised. Therefore, molecular and morphological research should be a permanent union in classical taxonomy.

The historical biogeography of *Trigonostemon* and *Dimorhocalyx* is analysed. A Bayesian dating analysis indicates that both genera originated in the Late Eocene to Oligocene. The S-DIVA and DEC analyses reveal the probable geographical origin and migration routes of the genera. *Trigonostemon* originated on the SE Asian mainland, but sect. *Trigonostemon* reached the Malay Peninsula through radiation in the Early to Middle Miocene. Diversification occurred subsequently in both SE Asian mainland and W Malesia. In contrast, *Dimorphocalyx* originated and diversified mostly on Borneo. In addition, the frequent change in sea levels during the Pleistocene accelerated the diversification of sect. *Trigonostemon* in Borneo and the Malay Peninsula.

The dot map of the georeferenced specimens (Figure 2) more or less reflects the species diversity and individual density of *Trigonostemon* among its distribution areas (as defined by Figure 43), although bias caused by collecting preferences exists (for distribution maps of *Dimorphocalyx*, see van Welzen & van Oostrum 2015). The connections in the floras of these areas depend largely on floristic exchanges (e.g., dispersals). Areas in West Malesia have a strong connection, partly because of the frequent dispersal events (for the detailed routes, see Chapter 7); in East Malesia, there appears a weak connection along the Outer Melanesian Arc, which was a chain of islands including part of the Philippines, N and E Sulawesi, N Moluccas, north coast of New Guinea and the Pacific Islands (nicely exemplified by de Boer 1995; the distributions of *Trigonostemon* and *Dimorphocalyx* more or less fits in with this island chain, except both genera are absent in Sulawesi); the Philippines acts as a bridge, connecting West and East Malesia. An indication of the study (although it is only a single case) is that the floristic compositions of Malesia are a dynamic network and cannot be simply demarcated by one single line (e.g., Wallace's line and other lines, also referred to as the area Wallacea, van Welzen et al. 2011). Future studies in biogeographic zones should not only focus on the static species occurrence, but also see from a dynamic angle and take the floristic exchanges into account.

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Summary

Trigonostemon is a plant genus in the family Euphorbiaceae comprising 59 species. These plants are small trees or shrubs growing in the lowland rainforests in Southeast Asia and the adjacent areas. The vegetative characters of these plants are often variable, but the small unisexual flowers with colourful petals (in both ♂ and ♀ flowers) and the 3 or 5 united stamens (in the ♂ flowers) are typical of the genus. The present thesis is a monograph of *Trigonostemon*, studying four aspects of the genus: the taxonomy, pollen morphology, molecular phylogeny and historical biogeography.

Trigonostemon was scientifically described by Carl Ludwig Blume in 1825. More than 140 species have been treated within the genus ever since. However, some of these species are identical to each other (synonyms) and some actually do not belong to the genus. The taxonomic studies revise the species based on observations of comparative morphology of herbarium and living material. The historical literature is compiled, and the characters that are useful in species delimitation are discussed. A total of 59 species (including 3 uncertain species) are accepted and scientifically described. Dichotomous identification keys, type information, geographical distributions and taxonomic notes are also provided (Chapters 2, 3, 4).

Pollen grains of plants differ by a vast array of shapes and sizes, as well as complex surface patterns and apertures (furrows and holes). The variation of the pollen grains often provides microscopic evidence for plant systematics. An exploration of the pollen morphology of *Trigonostemon* and its close relatives is made with light and electron microscopy. The pollen of a group of species in the Euphorbiaceae (often known as inaperturate crotonoids, *Trigonostemon* also belongs to this group) is characterised by a 'croton pattern' ornamentation (that consists of rings of five or six raised elements arranged around a circular area) on the surface. However, the 'croton pattern' ornamentation in the pollen of *Trigonostemon* is found to have reduced to spines or become completely absent in a number of species. The potential implication of the pollen morphology for the (infra)generic delimitation of *Trigonostemon* is discussed (Chapter 5).

Molecular phylogenetic studies use DNA sequences to evaluate the relationship between the species by modelling their evolutionary history. The DNA sequences of five regions of the plant genomes are used to reconstruct the phylogeny of *Trigonostemon*, *Dimorphocalyx* and other closely related species. Some previous studies argued that *Trigonostemon* and *Dimorphocalyx* should be merged into one single genus, but the molecular phylogeny shows that they are descendants of two different ancestors, and are thus two separate genera. Based on the molecular data and morphological characters, *Trigonostemon* is divided into four sections. The main characters used to define the sections are the division of stigmas, the apex of anthers, the shape of the nectar disc and the surface ornamentation of the pollen grains (Chapter 6).

Southeast Asia is the main distribution area of *Trigonostemon* and *Dimorphocalyx*. This area harbours a great biodiversity. The migration routes of plants and animals in this area have always been of great interest in biogeography. The historical biogeographic analyses have revealed that *Trigonostemon* and *Dimorphocalyx* originated at similar times (between the Oligocene and Early Miocene) but the two genera had different migration histories: *Trigonostemon* originated on the Southeast Asian mainland, expanded its distribution area to first the Malay Peninsular and then Borneo, and diversified in all these areas; in contrast, *Dimorphocalyx* originated and diversified mostly on Borneo. The Philippines is inferred to have played an important role in helping the plants to disperse to the east part of the Malay Archipelago. In addition, the frequent

changes of sea levels during the Ice Ages are considered to have propelled the diversification of *Trigonostemon* in Borneo and the Malay Peninsula (Chapter 7).

Samenvatting

Trigonostemon is een plantengeslacht in de familie Euphorbiaceae bestaande uit 59 soorten. Het zijn kleine bomen of struiken, die groeien in de laagland regenbossen in Zuidoost-Azië en aangrenzende gebieden. De vegetatieve kenmerken van deze planten zijn vaak variabel, maar de kleine eenslachtige bloemen met kleurrijke bloembladen (in zowel ♂ als ♀ bloemen) en de 3 of 5 verenigde meeldraden (in de ♂ bloemen) zijn kenmerkend voor het geslacht. Dit proefschrift is een monografie van *Trigonostemon*, die vier aspecten van het geslacht bestudeert: taxonomie, pollenmorfologie, een moleculaire fylogenie en historische biogeografie.

Trigonostemon werd wetenschappelijk beschreven door Carl Ludwig Blume in 1825. Sindsdien zijn er meer dan 140 soorten binnen het geslacht benoemd. Sommige van deze soorten zijn echter identiek aan elkaar (synoniemen) en sommige behoren niet tot het geslacht. De taxonomische studies reviseren de soorten op basis van vergelijkende morfologische waarnemingen aan herbarium en levend materiaal. De historische literatuur is verzameld en de kenmerken die bruikbaar zijn voor de afbakening van soorten worden besproken. Een totaal van 59 soorten (waaronder 3 dubieuze soorten) wordt geaccepteerd en wetenschappelijk beschreven. Dichotome determinatiesleutels, typegegevens, geografische verspreidingen en taxonomische notities worden eveneens gegeven (hoofdstukken 2, 3, 4).

Stuifmeelkorrels van planten verschillen in een breed scala aan vormen en grootten, evenals complexe oppervlaktepatronen en openingen (groeven en gaten). De variatie van de stuifmeelkorrels verschaft vaak microscopisch bewijs voor plantensystematiek. Een verkenning van de pollenmorfologie van *Trigonostemon* en zijn naaste verwanten wordt gemaakt met licht- en elektronenmicroscopie. Het stuifmeel van een groep soorten in de Euphorbiaceae (ook vaak bekend als inaperturate crotonoïden, *Trigonostemon* behoort tot deze groep) wordt gekenmerkt door een ‘crotonpatroon’ versiering op het oppervlak, welke bestaat uit ringen van vijf of zes verheven elementen die rond een cirkelvormig gebied zijn gerangschikt. De ‘croton ornamentatie’ van het stuifmeel van *Trigonostemon* blijkt echter te zijn gereduceerd tot stekels of volledig afwezig te zijn in een aantal soorten. De potentiële implicatie van de pollenmorfologie voor de (infra)generieke afbakening binnen *Trigonostemon* wordt besproken (hoofdstuk 5).

Moleculaire fylogenetische studies gebruiken DNA-sequenties om de relatie tussen de soorten te evalueren door hun evolutionaire geschiedenis te modelleren. De DNA-sequenties van vijf gebieden op het plantengenoom worden gebruikt voor het reconstrueren van de fylogenie van *Trigonostemon*, *Dimorphocalyx* en andere nauw verwante soorten. Sommige eerdere studies betoogden dat *Trigonostemon* en *Dimorphocalyx* moeten worden samengevoegd tot één enkel geslacht, maar de moleculaire fylogenie laat zien dat ze afstammen van twee verschillende voorouders en dus twee afzonderlijke geslachten zijn. Op basis van de moleculaire gegevens en morfologische kenmerken is *Trigonostemon* verdeeld in vier secties. De belangrijkste kenmerken, die worden gebruikt om de secties te definiëren zijn de verdeling van stigma’s, de top van de helmknoppen, de vorm van de nectarschijf en de oppervlakte ornamentatie van de stuifmeelkorrels (hoofdstuk 6).

Zuidoost-Azië is het belangrijkste verspreidingsgebied van *Trigonostemon* en *Dimorphocalyx*. Dit gebied herbergt een grote biodiversiteit. De migratieroutes van planten en dieren in dit gebied zijn altijd van grote interesse geweest voor biogeografie. De historische biogeografische analyses laten zien dat *Trigonostemon* en *Dimorphocalyx* op vergelijkbare tijden zijn ontstaan

(tussen het Oligoceen en het Vroege Mioceen) maar de twee genera hebben verschillende migratiegeschiedenissen: *Trigonostemon* ontstond op het Zuidoost-Aziatische vasteland, breidde zijn verspreidingsgebied uit naar het Maleise schiereiland en vervolgens naar Borneo, en diversifiëerde in al deze gebieden. *Dimorphocalyx*, daarentegen, is ontstaan op Borneo en vormde daar voornamelijk soorten. De Filippijnen worden geacht een belangrijke rol te hebben gespeeld bij het helpen verspreiden van de planten naar het oosten van de Maleise archipel. Bovendien wordt aangenomen dat de frequente veranderingen van de zeespiegel tijdens de ijstijden de diversificatie van *Trigonostemon* op Borneo en het Maleise Schiereiland te hebben versneld (hoofdstuk 7).

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Curriculum vitae

Ren-Yong Yu was born on 30 June 1989 in Beijing. He attended Beijing October First School and obtained his high school diploma in 2007. He aimed for a medical programme in the National College Entrance Examination, but was admitted to Sichuan University to study biology. His undergraduate thesis was about the observations of the behaviour of the Chinese monal (*Lophophorus lhuysii*, an endangered bird endemic to China). In 2011, he was awarded the bachelor's degree and then enrolled in a graduate programme at Sunyatsen University where he started specializing in plant taxonomy. A year later, he continued his study at the National Taiwan University and obtained his master's degree in 2014. His master's thesis was a taxonomic revision of the Thymelaeaceae in Taiwan. During his study, he carried out extensive field explorations in the mountains and gained firsthand experience in taxonomic research. Since 2015, he has been working as a PhD student at Naturalis Biodiversity Center. His work focused on the plant genus *Trigonostemon* Blume and formulates the present thesis. In the four years of studies, he paid visits to several herbaria in Europe and Asia, and he made several field trips to Southeast Asia to collect plant samples for the molecular analyses. The results of his research are all published (or accepted for publication) in scientific journals.

List of publications

Yu R-Y, van Welzen PC. 2018. A taxonomic revision of *Trigonostemon* Blume (Euphorbiaceae) in Malesia. Blumea 62: 179–229.

Yu R-Y, van der Ham R, van Welzen PC. 2019. Pollen morphology of *Trigonostemon* Blume and its relatives (Euphorbiaceae). Grana 58: 114–128.

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