

**REVISION AND PHYLOGENY OF SUBTRIBES  
CHROZOPHORINAE AND DORYXYLINAE (EUPHORBIACEAE)  
IN MALESIA AND THAILAND**

PETER C. VAN WELZEN

Rijksherbarium/Hortus Botanicus, P.O. Box 9514, 2300 RA Leiden, The Netherlands

SUMMARY

A phylogeny of the complete tribe Chrozophoreae is presented in order to establish the possible monophyly and relationships in subtribes Chrozophorinae (*Chrozophora*) and Doryxylinae (*Doryxylon*, *Melanolepis*, *Sumbaviopsis*, *Thyrsanthera*). Added are the other subtribes in tribe Chrozophoreae, the Speranskiinae (*Speranskia*) and Ditaxinae (*Argythamnia*, *Caperonia*, *Chiropetalum*, *Ditaxis*, *Philyra*). Outgroups are the genera *Agrostistachys* and *Chondrostylis* (tribe Agrostistachydeae).

The phylogeny shows two monophyletic groups, subtribe Speranskiinae together with Ditaxinae, and subtribe Chrozophorinae with Doryxylinae. The latter group is statistically well supported by a high bootstrap value. The first group is weakly supported and collapses easily when the characters are selected somewhat differently. The former subtribes Chrozophorinae and Doryxylinae are united into one subtribe, Chrozophorinae. The remaining taxa in tribe Chrozophoreae, the monogeneric subtribe Speranskiinae and subtribe Ditaxinae are united into subtribe Ditaxinae. Within subtribe Chrozophorinae s.l. *Chrozophora* is sister taxon to all other taxa, followed by *Thyrsanthera* and *Melanolepis*. *Doryxylon* and *Sumbaviopsis* were apparently the last to separate. The differences between all, mainly monotypic, genera are quite large, therefore, the present delimitation is favoured over a suggested union of *Doryxylon* and *Sumbaviopsis*.

**Key words:** *Chrozophora*, *Doryxylon*, *Sumbaviopsis*, *Thyrsanthera*, phylogeny, taxonomy.

INTRODUCTION

In the present classification of the Euphorbiaceae (Webster, 1994) tribe Chrozophoreae (subfamily Acalyphoideae), comprises four subtribes. Two subtribes are monogeneric, the Chinese Speranskiinae (*Speranskia* Baill.), and the Mediterranean to SE Asian Chrozophorinae (*Chrozophora* Neck. ex A. Juss.). Subtribe Ditaxinae comprises five genera, all American except for *Caperonia* A. St.-Hil., which is also found in Africa; the other genera are *Argythamnia* P. Br., *Chiropetalum* A. Juss., *Ditaxis* Vahl ex A. Juss., and *Philyra* Klotzsch. Ingram (1980a) united *Argythamnia*, *Chiropetalum*, and *Ditaxis*, but recognised the three taxa at subgenus level and presented a revision of subgenus *Chiropetalum* (Ingram, 1980b). Webster (1994) points out that the three taxa are morphologically and palynologically distinct and he still recognises them at the genus level. The fourth subtribe, Doryxylinae, is SE Asian and Malesian, and comprises four genera, *Doryxylon* Zoll., *Melanolepis* Rchb.f. & Zoll., *Sumbaviopsis* J.J. Sm., and *Thyrsanthera* Pierre ex Gagnep. All genera are monotypic except for *Melanolepis*, which includes two species. Balakrishnan (1967) suggests that *Doryxylon* and *Sumbaviopsis* can easily be united.

A revision of the Malesian and Thai species of Doryxylinae and Chrozophorinae will be presented except for *Melanolepis* which is published separately as it is a joined venture of four authors (Van Welzen et al., 1999). The phylogeny of the subtribes will be analysed in conjunction with the other two subtribes, otherwise no well supported opinion can be presented on the possible monophyly of tribes Doryxylinae and/or Chrozophorinae.

#### PHYLOGENY AND CLASSIFICATION OF TRIBE CHROZOPHOREAE

All characters are treated as unordered. The phylogenetic analysis was performed with PAUP 3.1.1 (Swofford, 1993), options: branch and bound, mulpars, minimal trees, addition sequence furthest. Character optimisation was studied with MacClade version 3 (Maddison & Maddison, 1992). The bootstrap values (Felsenstein, 1985) were obtained (1000 replicates, branch and bound, further default settings of PAUP). Decay indices (Bremer, 1988) were obtained by comparing the resolved branches in strict consensus trees of cladograms up to 4 steps longer with the most parsimonious cladogram.

The analysis is based on 24 characters (see Table 1 for data matrix):

1. Habit: 1 = herb/shrub; 2 = shrub/tree.

The seeming overlap between both states is caused by the fact that the herbs obtain woody stems and become shrub-like and the trees already flower when they are still in the shrub phase.

2. Dio-/monoecy: 1 = dioecious; 2 = monoecious.

Sometimes monoecy is difficult to observe because several specimens only show one sex. In these cases sheets with both sexes on the same plant are taken as exemplary for the species.

3. Indumentum: 1 = simple hairs only; 2 = malpighiaceus; 3 = stellate (lepidote). All species show simple hairs, but several have malpighiaceus hairs (T-shaped hairs; mainly subtribe Ditaxinae) or stellate hairs in addition (subtribes Chrozophorinae and Doryxylinae; *Chrozophora* has either stellate or lepidote hairs). The only polytypic genus is *Chiropetalum* (subtribe Ditaxinae) with malpighiaceus or stellate hairs next to simple hairs.

4. Petiole length: 1 = less than 2 cm long or absent; 2 = (1–)2–31 cm long.

Most members of subtribes Ditaxinae and Speranskiinae have short petioles (*Caperonia* and *Speranskia* are polymorphic) and subtribes Chrozophorinae and Doryxylinae have much longer petioles, especially those of the large mature leaves (the overlap in both states is caused by the smaller younger leaves in the latter two sections).

5. Petiole pulvination: 1 = not pulvinate; 2 = basally pulvinate; 3 = basally and apically pulvinate.

The outgroups are basally pulvinate, all others are not pulvinate except for *Doryxylon* and *Sumbaviopsis* which are apically and basally somewhat pulvinate.

6. Petiole ribs: 1 = absent when dry; 2 = present when dry.

The petioles of *Doryxylon* and *Sumbaviopsis* become very distinctly ribbed in dried condition.

7. Leaf peltation: 1 = absent; 2 = present.  
*Sumbaviopsis* is the only genus with leaves which are always somewhat peltate; those of *Doryxylon* are often peltate, but they are scored as always peltate, because peltation may be a synapomorphy for both genera.
8. Marginal teeth: 1 = eglandular; 2 = glands at end of teeth; 3 = glands on abaxial side of teeth.  
 The two outgroups and part of subtribe Doryxylinae have marginal teeth which end in glands. *Speranskia* has the glands at the abaxial surface of the teeth.
9. Marginal teeth: 1 = without mucro; 2 = with mucro.  
 The marginal teeth of *Argythamnia*, *Chiropetalum* and *Ditaxis* end in a mucro which does not appear to be glandular. Therefore, the presence of the mucro is treated as a separate character and it is not regarded as character state 2 of the former character.
10. Group of basal adaxial glands: 1 = absent; 2 = group adaxially.  
 The leaves of *Melanolepis* (subtribe Doryxylinae) always show a basal group of adaxial glands. In *Doryxylon* (subtribe Doryxylinae) this group of glands is present (leaves not peltate) or absent (leaves peltate); they are coded as always present as this character may provide an apomorphy for both genera.
11. Glands on lamina: 1 = absent (or few adaxially); 2 = yellow, abaxially.  
 Subtribes Chrozophorinae and Doryxylinae except for *Doryxylon* have yellow glands at the abaxial leaf surface.
12. Venation: 1 = pinnate; 2 = palmate.  
 Subtribe Doryxylinae have a basally palmate venation.
13. Inflorescence position: 1 = axillary; 2 = terminal.  
 The inflorescences of *Speranskia* (subtribe Speranskiinae) and of the members of subtribes Chrozophorinae and Doryxylinae are terminal, they are axillary in all other taxa.
14. Fusion of staminate petals: 1 = free; 2 = basally fused with androphore.  
 The petals of *Argythamnia*, *Chiropetalum* and *Ditaxis* (subtribe Ditaxinae) are fused with the androphore. A question mark has been scored for *Chondrostylis*, because this taxon lacks petals.
15. Staminate disc: 1 = absent; 2 = outside stamens; 3 = among stamens.  
 An extrastaminal disc is present in most staminate flowers, only in *Chondrostylis* the disc glands are found among the stamens.
16. Number of stamens: 1 = 3–16; 2 = c. 30; 3 = 40–75; 4 = 100–250.  
 The number of stamens is low in *Agrostistachys*, the Speranskiinae, Ditaxinae, and Chrozophorinae. Only in *Chondrostylis* and especially in the Doryxylinae very high numbers can be found.
17. Stamen type: 1 = *Agrostistachys* type; 2 = normal type.  
 The *Agrostistachys* type (connective enlarged, anther sacs pendulous) is found in the outgroups, *Agrostistachys* and *Chondrostylis*. All other taxa show normal anthers with a narrow connective and non-pendulous thecae.
18. Pollen texture: 1 = heterobrochate; 2 = not distinctly heterobrochate; 3 = psilate.  
 The pollen texture of subtribes Doryxylinae, Chrozophorinae, and *Agrostistachys* is heterobrochate, indistinctly heterobrochate in the other taxa of tribe Chrozophoreae and psilate in *Chondrostylis* (Punt, 1962; Webster, 1994).

19. Pistillate petals: 1 = absent; 2 = present.  
Petals in pistillate flowers are absent in subtribe Doryxylinae and in *Chondrostylis*.
20. Pistillate disc: 1 = absent; 2 = annular; 3 = separate lobes.  
The pistillate disc is absent in *Caperonia* (subtribe Ditaxinae) and *Sumbaviopsis*, it is annular in the other members of subtribe Doryxylinae, and in subtribes Chrozophorinae, and Speranskiinae; the disc is lobed in subtribe Ditaxinae. *Agrostistachys* and *Argythamnia* (subtribe Ditaxinae) are polymorphic, some species have annular discs, others have separate lobes.
21. Ovary: 1 = not muriculate; 2 = muriculate (in part of species).  
The ovary of *Speranskia* (subtribe Speranskiinae) and *Caperonia* (subtribe Ditaxinae) is (often) muriculate.
22. Stigmatic papillae: 1 = absent; 2 = long, thick, round; 3 = long, slender, round; 4 = knobs; 5 = broad and flat (strap-like).  
Subtribes Chrozophorinae and Doryxylinae show long and slender papillae on the stigmas. Subtribe Ditaxinae shows no apparent papillae, while *Speranskia* (subtribe Speranskiinae) has broad, flat papillae. The outgroups have short knobs (*Agrostistachys*) or long and thick papillae (*Chondrostylis*).
23. Fruits containing red dye: 1 = absent; 2 = present.  
Dried fruits which are boiled show red dye when the fruit is somewhat damaged. The dye is absent in the outgroups and several members of subtribe Doryxylinae (*Doryxylon*, *Sumbaviopsis*, and *Thyrsanthera*). It is unknown in *Speranskia* (subtribe Speranskiinae).
24. Seeds: 1 = without fleshy appendages; 2 = sarcotesta present.  
A thin sarcotesta is present in subtribes Chrozophorinae and Doryxylinae. All other taxa have seeds without fleshy appendages.

Table 1. Data matrix for the phylogenetic analysis of the tribe Chrozophoreae with *Agrostistachys* and *Chondrostylis* as outgroups. In cases of polymorphism the primitive character state (deduced after the analysis) is indicated in bold.

Taxa \ Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
Outgroups:																									
<i>Agrostistachys</i>	2	1	1	1	2	1	1	2	1	1	1	1	1	2	1	1	1	2	<b>2&amp;3</b>	1	4	1	1		
<i>Chondrostylis</i>	2	1	1	<b>1&amp;2</b>	2	1	1	2	1	1	1	1	1	?	3	2	1	3	1	2	1	2	1	1	
Speranskiinae																									
<i>Speranskia</i>	1	2	1	<b>1&amp;2</b>	1	1	1	3	1	1	1	1	2	1	2	1	2	2	2	2	2	5	?	1	
Ditaxinae																									
<i>Argythamnia</i>	1	2	2	1	1	1	1	2	1	1	1	1	2	2	1	2	2	2	<b>2&amp;3</b>	1	1	2	1		
<i>Caperonia</i>	1	2	1	<b>1&amp;2</b>	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	2	1	2	1		
<i>Chiropetalum</i>	1	2	<b>2&amp;3</b>	1	1	1	1	2	1	1	1	1	2	2	1	2	2	2	3	1	1	2	1		
<i>Ditaxis</i>	1	2	2	1	1	1	1	2	1	1	1	1	2	2	1	2	2	2	3	1	1	2	1		
<i>Philyra</i>	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	2	2	2	3	1	1	2	1		
Chrozophorinae																									
<i>Chrozophora</i>	2	2	3	2	1	1	1	1	1	2	1	2	1	2	1	2	1	2	2	1	3	2	2		
Doryxylinae																									
<i>Doryxylon</i>	2	2	3	2	3	2	2	2	1	2	2	2	2	1	1	4	2	1	1	2	1	3	1	2	
<i>Melanolepis</i>	2	2	3	2	1	1	1	2	1	2	2	2	2	?	1	4	2	1	1	2	1	3	2	2	
<i>Sumbaviopsis</i>	2	2	3	2	3	2	2	2	1	1	2	2	2	1	1	3	2	1	1	1	1	3	1	2	
<i>Thyrsanthera</i>	2	2	3	2	1	1	1	1	1	2	2	2	2	1	2	3	2	1	1	2	1	3	1	2	

Several characters have been excluded from the analysis (sometimes after the first analysis), because they only provide (parallel) autapomorphies:

*Agrostistachys*: pistillode present.

*Caperonia*: branches thick and hollow; stinging hairs present; pollen 6-colporate; pistillode present; pistillate sepals imbricate.

*Chiropetalum*: apex of staminate petals usually with coarse teeth; colpi with operculum.

*Chondrostylis*: glands at apex of petiole; panicle; staminate petals absent.

*Chrozophora*: leaves often lobed; usually 2 abaxial glands near leaf blade insertion; staminate sepals basally united; anthers 4-locular.

*Ditaxis*: pollen bi-laterally symmetric.

*Doryxylon*: thorns of axillary bud origin; apex of staminate petals frayed.

*Melanolepis*: leaves lobed; panicles; sexes on different inflorescences; staminate petals absent; connective with abaxial gland.

*Philyra*: thorns of stipular origin; gynophore present; staminodes present.

*Sumbaviopsis*: sexes on different inflorescences; staminate flowers with torus; pistillate sepals imbricate.

The phylogenetic analysis resulted in a single cladogram (Fig. 1) of 54 steps (including 6 steps for the polymorphic taxa, the primitive states, as indicated by PAUP, are in bold in Table 1),  $ci = 0.759$ ,  $ri = 0.817$ . The cladogram shows a statistically significant support for the Chrozophoreae as a tribe (bootstrap = 96%), but this is probably exaggerated as only character 23 is very typical for tribe Chrozophoreae (red dye in the fruits). Next the cladogram splits into two major groups, subtribes *Speranskiinae* and *Ditaxinae* together, and subtribe *Chrozophorinae* together with subtribe *Doryxylinae*. The first group is very unstable, slightly altered characters provide very different positions for *Speranskia* and *Caperonia*, either basal to all other Chrozophoreae or even basal to the second group. The instability of the group is already indicated by the low bootstrap values. Subtribe *Chrozophorinae* together with subtribe *Doryxylinae* have much higher bootstraps, but never 95% (Felsenstein, 1985). However, recently (Hillis & Bull, 1993; Felsenstein & Kishino, 1993) it was empirically demonstrated that bootstrap values of 70% and higher correspond to a probability of 95% (and higher) that the clade is real (the opposite is true for lower bootstrap values, these do not underestimate but exaggerate the reliability of clades). This means that all monophyletic groups in the Chrozophorinae–Doryxylinae clade have statistically significant bootstrap values. First to split off in this clade is *Chrozophora*, followed by *Thyrsanthera* and *Melanolepis*, respectively. The closest sister group relations are shown by *Doryxylon* and *Sumbaviopsis*. In the other major clade *Speranskia* and *Caperonia* are sister genera (weak support, only the murication of the ovaries) and *Philyra* is sister group to the remaining three genera in subtribe *Ditaxinae*. The latter group, *Argythamnia*, *Chiropetalum*, and *Ditaxis*, show a significant bootstrap, even though their inner relationships are not resolved. This supports Ingram's monogeneric view of these three genera (Ingram, 1980a).

The Decay Indices also support some of the clades. Especially the basal node is well supported, present in the consensus of 1166 trees with up to 3 steps more than the most parsimonious cladogram. The Chrozophorinae and Doryxylinae clade is supported by a Decay Index of 2 (clade still present in 377 trees of up to 2 steps more

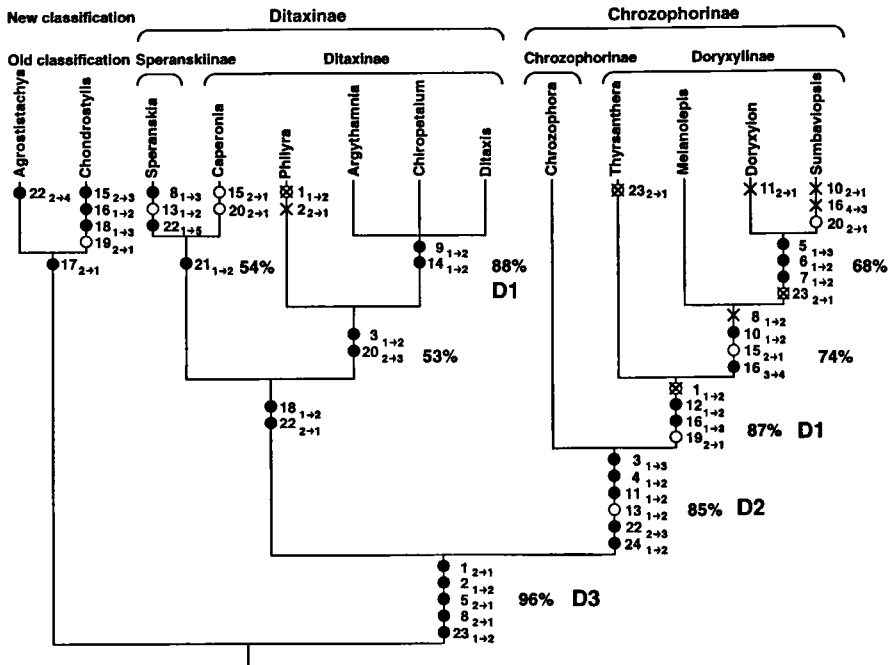


Fig. 1. Single most parsimonious cladogram for the tribe Chrozophoreae. Bootstrap values over 50% are indicated with percentages, decay indices with a capital D. Black dots = apomorphies; white dots = parallel apomorphies; crosses = reversals; white dots with cross = parallel reversals.

than the most parsimonious cladogram), and the Doryxyliinae and the *Argythamnia* group are supported by a D1 level.

Geography supports the cladogram. All SE Asian taxa are united in subtribe Doryxyliinae, while together they are grouped with the Mediterranean/N African to SE Asian *Chrozophora*. All American taxa are together in subtribe Ditaxinae, including the partially African (W Africa to Ethiopia) *Caperonia*. Included in the latter group, and geographically somewhat out of place, is the Chinese *Speranskia*. However, the position of *Caperonia* and *Speranskia* in the cladogram is uncertain, they can also be basal to the Chrozophorinae + Doryxyliinae or basal to all Chrozophoreae in which case they agree very well geographically with the other groups.

The delimitation within the Chrozophoreae has to change. It is obvious that the monogeneric subtribe Chrozophorinae has to be united with subtribe Doryxyliinae and this decision is made here. This decision agrees with Webster's observation (1994) that *Thyrsanthera* is intermediate between subtribes Chrozophorinae and Doryxyliinae. This subtribal group has to be called Chrozophorinae as this is the oldest available and valid name. Likewise, the monogeneric subtribe Speranskiinae has to be united with subtribe Ditaxinae and called Ditaxinae. However, this group may not be monophyletic but can be paraphyletic; only a more extensive analysis may prove the possible monophyly.

Within the Chrozophorinae (s.l.) most genera are monotypic, i.e., *Thyrsanthera*, *Doryxylon*, and *Sumbaviopsis*. Monotypic genera only stress the fact that they are

relatively more different from other taxa, but their delimitation does not indicate any information about relationships. An alternative is to unite *Doryxylon*, *Melanolepis*, *Sumbaviopsis*, and *Thyrsanthera* into a single genus, but this will only result in unwanted name changes. The best alternative is to use Nelson's sequence rule (1974) in discriminating monophyletic genera (as far as this is possible in a Linnaean classification; see discussion in Van Welzen, 1998). This means that *Thyrsanthera* and *Melanolepis* remain separate genera and that for *Doryxylon* and *Sumbaviopsis* Balakrishnan's suggestion of a union has to be evaluated.

Balakrishnan (1967) discussed that *Sumbaviopsis albicans* should be sunk into the genus *Doryxylon*, which then would comprise two species. According to him *Doryxylon spinosum* only differs from *Sumbaviopsis albicans* in the presence of spines and less important characters like smaller non-peltate leaves (incorrect, often peltate) with more dentation, shorter racemes, and shorter pedicels in fruit. In fact there are more differences, pistillate flowers in *Doryxylon spinosum* have a disc, while the receptacle in the staminate flowers does not appear to be torus-like as in *Sumbaviopsis albicans* (though no mature flowers could be studied in *Doryxylon*), the number of stamens is much higher in *Doryxylon spinosum*, and the leaves in *Doryxylon spinosum* lack the round yellow glands at the lower surface. The phylogenetic analysis shows that Balakrishnan is correct in uniting the two, because they are sister species. However, two other reasons exist to maintain the status quo. The differences between *Doryxylon spinosum* and *Sumbaviopsis albicans* are much larger than is usually the case between species within Euphorbiaceae genera (e.g., compare the small differences between the two species in *Melanolepis*). Usually, the differences between the species are very slight, even up to the level that a phylogenetic analysis is impossible. Secondly, uniting both genera means a name change for the most common and widespread species (*Sumbaviopsis albicans*) of the two and it, again, confirms the instability of our classification. Because of these two reasons, even in spite of the fact that I like to invoke phylogenetic classifications as much as possible, I am in favour of keeping both species separated in different genera.

This means that the only changes in delimitation are at the subtribal level, no changes are suggested at the generic level, except perhaps to follow Ingram's view (1980a) of a united genus *Argythamnia*.

### Subtribe Chrozophorinae

A brief description of tribe Chrozophoreae and subtribes Chrozophorinae and Doryxylineae can be found in Webster (1994). Here a key to the genera and a revision of the Malesian and Thai species of *Chrozophora*, *Doryxylon*, *Sumbaviopsis*, and *Thyrsanthera* is presented; a treatment of *Melanolepis* can be found in the phylogeny, and for the taxonomy see Van Welzen et al. (1999).

#### KEY TO THE GENERA

- 1a. Stamens free, connective with apicidorsal gland. Leaves not peltate, basally with an adaxial group of glands, 5–38 by 5–34 cm; petiole not pulvinate, usually basally constricted when dry ..... *Melanolepis (multiglandulosa)*

- b. Stamens free or united, connective without gland. Leaves peltate or not, basally with or without an adaxial group of glands; when glands are present: leaves 2.8–12 by 2.2–12 cm, and the petiole basally and apically somewhat pulvinate . . . 2
- 2a. Herb or shrub. Leaves usually 3-lobed; margin entire, without glands; with 2 abaxial glands near petiole insertion. Stamens 3–16, united. Pistillate flowers with petals. Fruit producing red dye . . . . . **Chrozophora (rotleri)**
- b. Shrub or tree. Leaves not lobed; margin entire or dentate and then with glands; without abaxial glands near petiole insertion. Stamens 40–250, united or free. Pistillate flowers without petals. Fruit lacking red dye . . . . . 3
- 3a. Leaves not peltate; margin entire, without glandular teeth; petiole not pulvinate. Stamens united; staminate disc present . . . . . **Thyrsanthera (suborbicularis)**
- b. Leaves usually peltate; margin subentire to dentate, with glandular teeth; petiole basally and apically somewhat pulvinate. Stamens free; staminate disc absent 4
- 4a. Thorns often present (modified axillary buds). Leaves often peltate, 2.8–12 by 2.2–12 cm, without yellow glands on lower surface. Staminate flowers without torus; stamens 110–130. Pistillate disc present . . . . . **Doryxylon (spinosum)**
- b. Thorns absent. Leaves always peltate, 6.8–37 by 3.2–19 cm, with yellow glands on lower surface. Staminate flowers with torus; stamens c. 75. Pistillate disc absent . . . . . **Sumbaviopsis (albicans)**

### CHROZOPHORA

The type species of *Chrozophora* Neck. ex A. Juss., *C. tinctoria* (L.) A. Juss., has been known since antiquity. The fruits provide a beautiful red dye (called turn-sole dye, bezetta rubra, or tournesol), which is used in liqueurs, wine, pastries, linen, and the peel around Dutch cheeses. Originally, Linnaeus (1753) referred this species to *Croton*, following a suggestion made by his Dutch friend Van Royen. Since then various authors recognised it as a separate genus and various names have been (often invalidly) applied. Finally, the name *Chrozophora* Neck. ex A. Juss. was conserved against *Tournesol* Adans. (no. 4355 in the ICBN). Prain (1918) provides a lengthy account of the history of the genus and also of the various species.

Prain (1918) was also the last to publish a full revision of the genus. He divides the genus into two sections (*Trichocarpa* with stellate hairs on the carpels and *Lepidocarpa* with lepidote hairs on the carpels; *Lepidocarpa* is an invalid name, should be section *Chrozophora* – autonym rule). The two sections are each further subdivided into two ‘forms’. This revision only treats *C. rotleri* (Geiseler) A. Juss. ex Spreng., because it is the only species present in Thailand and Malesia. *Chrozophora rotleri* is classified in section *Trichocarpa*, ‘form’ *Plicatae*.

Typical characters of this genus are (see also Webster, 1994): Herbs or small shrubs; monoecious; indumentum of stellate or lepidote hairs next to simple hairs; leaves alternate, simple, often 3-lobed, laxly crenate, usually with 2 abaxial, subbasal glands; inflorescences terminal, basally with pistillate flowers, apically with staminate flowers; flowers 5-merous, calyx basally united; petals present; disc very indistinct, lobed in staminate flowers, annular and very flat in pistillate flowers; stamens 13–16, united, splitting off in two or three groups; pollen grains heterobrochate, stephanocolporate; fruit a rhegma; seeds carunculate and partly covered by a sarcotesta.



**Chrozophora** Neck. ex A. Juss.

*Chrozophora* Neck. ex A. Juss., Euphorb. Gen. (1824) 27 ('*Crozophora*'), nom. & orth. cons.; Müll. Arg. in DC., Prodr. 15, 2 (1866) 746; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vi (1912) 17; Prain, Bull. Misc. Inform. (1918) 49; Airy Shaw, Kew Bull. 26 (1972) 232; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 73. — Type species: *Croton tinctorium* L. [= *Chrozophora tinctoria* (L.) A. Juss.].

Herb or undershrub, monoecious. *Indumentum* consisting of very dense, sessile and peduncled stellate or lepidote hairs, next to simple hairs (latter mainly on lower leaf surface). *Stipules* narrowly triangular, tomentose, caducous, scars very indistinct. *Leaves* spirally arranged, simple; petiole not pulvinate, reniform in transverse section; blade ovate, often 3-lobed, coriaceous, symmetric, margin shallowly to laxly but distinctly crenate, apex rounded, upper surface less densely covered by hairs than lower surface, the latter usually basally with 2 glands near insertion and often with submarginal glands, glands crater-like (circular, rim-like wall, concave inside); venation basally trinerved, pinnate along midrib with nerves ending open in the margin, veins laxly scalariform, quaternary veins reticulate. *Inflorescences* terminal racemes (in fruit pseudo-lateral and opposite to leaf due to extension of axillary buds), solitary (or 2 together), not branching, basal flowers pistillate, apical ones staminate; rachis tomentose. *Bracts* narrowly triangular, only hairy outside. *Flowers* actinomorphic, staminate flowers usually 2 per node, pistillate flowers usually single; pedicels with abscission zone; calyx 5-lobed, valvate, tomentose outside, glabrous inside; petals 5; disc indistinct, glabrous. *Staminate flowers* subsessile; calyx campanulate, lobes ovate; petals slightly larger than sepals, obovate, petaloid, margin in upper part undulate, with simple hairs on both sides; disc divided into small glands, united with petals; stamens 13–16, glabrous, filaments united into a column, branching off in c. 3 layers, free part thread-like, anthers basidorsifixed, 4-locular, opening extrorse with lengthwise slits; pistillode absent. *Pistillate flowers* pedicellate; calyx and petals persistent, both 5-merous, narrowly ovate, hairy outside, glabrous inside, petals sepaloid in texture, slightly smaller than calyx; disc annular, very flat; pistil 3-locular, on short gynophore, one ovule per locule, smooth, covered by flat stellate hairs; style short, hairy, persistent; stigmas almost completely divided, below stellately hairy, above with long slender papillae, persistent. *Fruits* slightly lobed capsules, triangular in transverse section, dehiscing usually septicidally and partly loculicidally into 3 bivalved parts, outside densely stellate, inside glabrous, thin-walled; column slender, with frayed remnants of the septa, apically triangular; septa single veined?. *Seeds* 3 per fruit, obovate, angular; covered by a thin, incomplete sarcotesta; the latter carunculate apically. *Embryo* flat; endosperm copious.

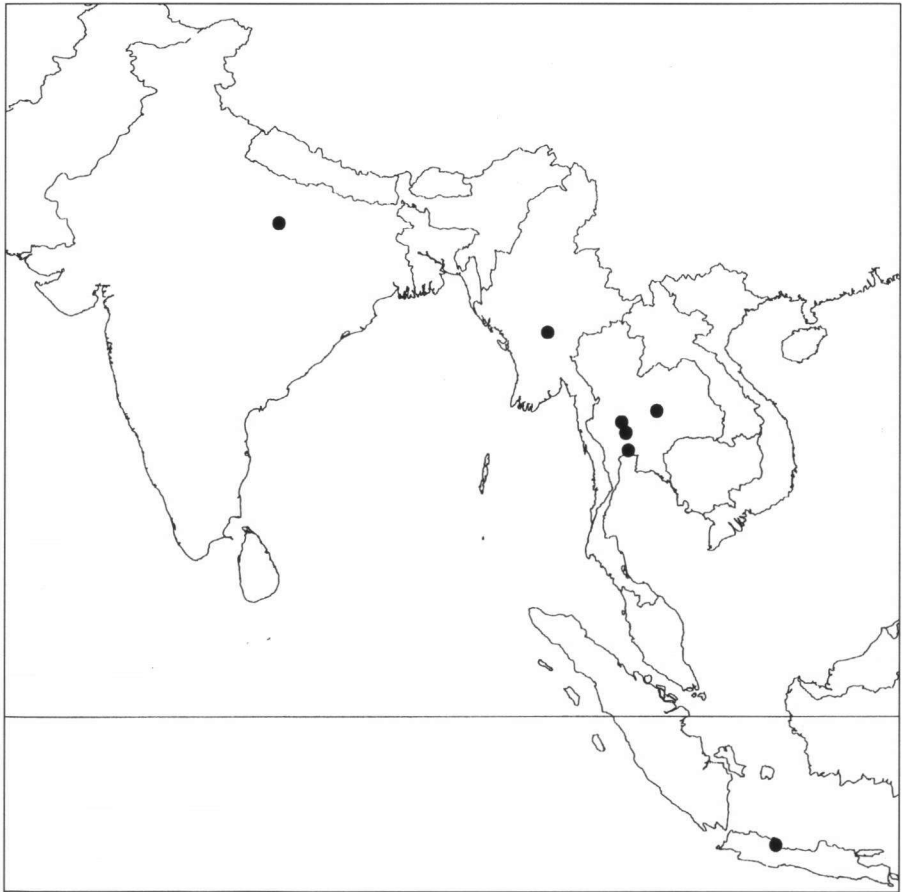
Distribution — Eleven species from Africa and the Mediterranean through SW and S Asia to SE Asia. In Malesia a single species, probably accidentally introduced into Central Java.

**Chrozophora rottleri** (Geiseler) A. Juss. ex Spreng. — Fig. 2, Map 1

*Chrozophora rottleri* (Geiseler) A. Juss. ex Spreng., Syst. Veg. 3 (1826) 850; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vi (1912) 19; Prain, Bull. Misc. Inform. (1918) 95 (see there for full synonymy); Steenis, Bull. Jard. Bot. Buitenzorg III, 17 (1948) 399; Nath, Bot. Surv. S. Shan

States (1960) 109; Backer & Bakh.f., Fl. Java 1 (1964) 477. — *Croton rottleri* Geiseler, Croton Monogr. (1807) 54; A. Juss., Euphorb. Tent. (1824) 28. — *Chrozophora plicata* (Vahl) A. Juss. ex Spreng. var. *rottleri* (Geiseler) Müll. Arg. in DC., Prodr. 15, 2 (1866) 747. — Type: Vahl s.n., s.d. (C, n.v.; IDC microfiche 2201-1).

Herb to undershrub, up to 60 cm high; flowering twigs 2–2.5 mm thick. *Indumentum* consisting of stellate and (few) simple hairs. *Stipules* 1.3–2.7 by c. 0.3 mm. *Leaves*: petiole 0.8–5.5 cm long; blade ovate, not to usually distinctly 3-lobed, 2.6–9 by 2.6–9 cm, index 1–1.9, pale green, base obtuse to usually emarginate, margin without distinct glands, lower surface with 2 glands near the base, 1 mm diam., and usually several smaller ones submarginally, venation impressed above, raised below, nerves c. 4 per side. *Inflorescences* up to 4 cm long, elongating in fruit to up to 10 cm long. *Bracts* very inconspicuous to c. 1.6 by 0.3 mm. *Staminate flowers* 4–6 mm diam., yellow; calyx white, united part c. 1 mm high, lobes 3.2–4 by c. 1.2 mm; petals 3.7–3.8 by 1.5–1.6 mm; androphore 3.3–3.8 mm long, basal 1.2–1.3 mm without filaments; filaments 0.3–0.8 mm long; anthers 0.9–1.3 by c. 0.7 mm, yellow. *Pistillate*



Map 1. Distribution of *Chrozophora rottleri* (Geiseler) A. Juss. ex Spreng.

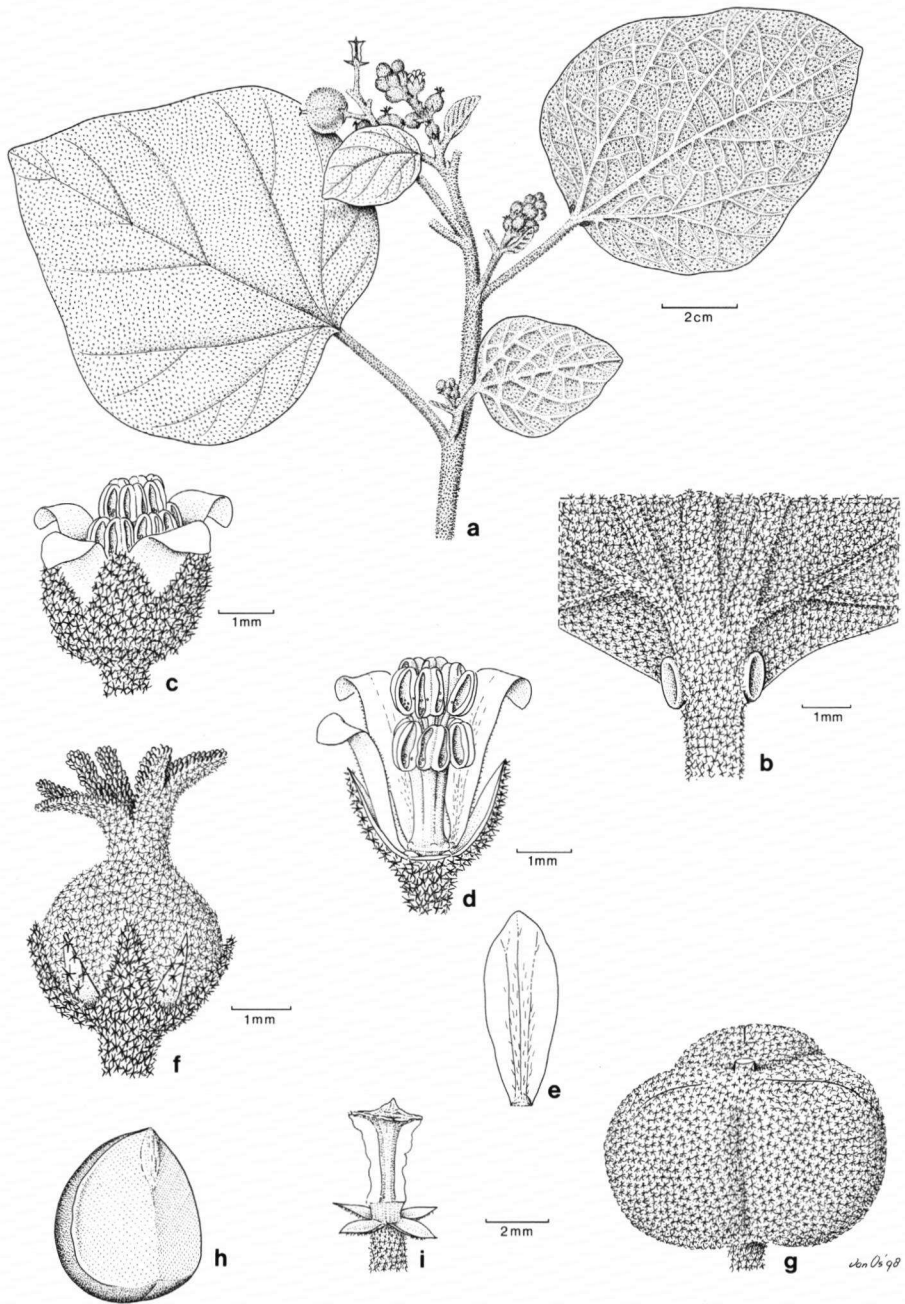


Fig. 2. *Chrozophora rotleri* (Geiseler) A. Juss. ex Spreng. a. Habit; b. abaxial basal leaf glands; c. staminate flower; d. staminate flower with a few sepals and petals removed showing united stamens; e. staminate petal; f. pistillate flower; g. fruit; h. seed; i. fruit column after dehiscence [a–g: Kerr 5725; h, i: Maxwell 71-302; all L].

flowers 3.2–3.3 mm diam., (greenish to) yellow; pedicel 1.4–2 mm long, elongating in fruit to up to 1.1 cm; calyx lobes only basally united, 1.5–2.2 by 0.5–0.7 mm; petals 1.3–2 by 0.4–0.6 mm; ovary ovoid, 2.7–3 by 2.2–3 mm wide; style 0.5–0.8 mm long, red, stigmas erect, up to 2.3 mm long, apically split for up to 1.8 mm, red. Fruits 8–9 by c. 5 mm; column after dehiscence 3–3.5 mm long. Seeds 3.8–3.9 by 3.2–3.6 by 3–3.2 mm.

Distribution — India, Myanmar, Thailand, Andaman Islands, and Malesia: Central Java. The plant has probably been introduced accidentally into Java, because it is only known from an area of a sugar cane factory.

Ecology & Habitat — Locally common in wet places like waste areas, along roads, and along and in stream beds. Soil: clay (mud), sand. Altitude 10–200 m. Flowering and fruiting: December–September, but perhaps the whole year through.

Uses — The fruits provide a blue-colouring dye, though the plant has never been cultivated for this purpose.

Note — *Chrozophora plicata* (Vahl) A. Juss. ex Spreng. is often confused with *C. rottleri*, because one of the first leads in Prain's key (1918) asks for the length of the inflorescence relative to the surrounding leaves. The inflorescence should be shorter than the leaves in *C. plicata* and longer in *C. rottleri*. However, they are only longer in *C. rottleri* when the inflorescences are old and have shed their seeds. The best character to separate both species is in the stellate hairs on the ovary/fruit, these hairs are flat, 2-dimensional, almost lepidote in *C. rottleri* (lacking the patent hairs), and normal, 3-dimensional in *C. plicata*. Furthermore, the leaf blades in *C. plicata* are usually smaller (less than 3 cm long) and of a much darker green (at least when dry).

## DORYXYLON

Zollinger established the genus *Doryxylon* in 1857, with *D. spinosum* as the only species based on material from Sumbawa in the Lesser Sunda Islands of Indonesia (Zollinger 3341). Baillon (1858), probably unaware of Zollinger's publication, used the same type specimen (but presumably another duplicate) to describe his monotypic genus *Sumbavia* (with *Sumbavia rottleroides*), thus creating a superfluous name.

Philippine material was independently described by Blanco (1837) as *Adelia acidoton* (non Linnaeus), to which Náves (1877–1883) added the superfluous name *Mercadoa mandalojonensis*.

Baillon's name was mainly used until Merrill (1918) tried to interpret Blanco's name. Merrill then correctly interpreted the various names and selected Zollinger's name as the accepted name.

A problem in the study of *Doryxylon* is the fact that no specimens with mature staminate or pistillate flowers have ever been collected. Therefore, the strange character found in *Sumbaviopsis*, a torus in the staminate flowers, could not be observed in *Doryxylon*. Typical characters of *Doryxylon* are its monoecy, the petioles, inflorescences, and pedicels with longitudinal grooves when dry, though less so as in *Sumbaviopsis*, the stems with a broad soft pith, the axillary buds which may develop into thorns, the mainly ovate leaves which are dentate, the glands at the apex of the marginal teeth, which may be grouped basally as in *Melanolepis*, the stellate indumentum, the presence of petals in staminate flowers, the many free stamens, the absence of a sta-

minate disc, 3-colporate heterobrochate pollen, the imbricate pistillate sepals, the presence of a disc in pistillate flowers, the 3- (or 4-)locular ovaries, the short style with entire, recurved stigmas, the hardly lobed, brown capsules, and the presence of a thin sarcotesta.

The species has a disjunct distribution, but the Philippines specimens hardly differ from the ones of the Lesser Sunda Islands. The latter usually have no peltate leaves, more pronounced glands along the leaf margins and a somewhat darker brown indumentum on the inflorescences.

### **Doryxylon Zoll.**

*Doryxylon* Zoll., *Natuurk. Tijdschr. Ned.-Indië* 14 (1857) 172; *Linnaea* 29 (1859) 469; Merr., *Sp. Blancoan.* (1918) 221; Airy Shaw, *Kew Bull.* 37 (1982) 16; *Alph. Enum. Euphorb. Philipp. Is.* (1983) 21; G.L. Webster, *Ann. Missouri Bot. Gard.* 81 (1994) 72. — Type species: *Doryxylon spinosum* Zoll.

*Sumbavia* Baill., *Étude Euphorb.* (1858) 390; Müll. Arg. in DC., *Prodr.* 15, 2 (1866) 727; Pax & K. Hoffm. in Engl., *Pflanzenr.* IV.147.vi (1912) 12. — Type species: *Sumbavia rottleroides* Baill. [= *Doryxylon spinosum* Zoll.].

[*Mercadoa* Náves in Blanco, *Fl. Filip.*, ed. 3 (1877–1883) t. 463, nom. nud. — Based on *Mercadoa mandalajonensis* Náves = *Doryxylon spinosum* Zoll.]

(Shrub to) tree, probably monoecious, but usually only one sex per plant; flowering twigs smooth, very shortly tomentose when young, lenticellate, with a broad soft pith. *Indumentum* consisting of simple and stellate hairs. *Stipules* triangular, densely hairy outside except for the probably glandular apex, glabrous inside, early caducous, scars very indistinct. *Leaves* spirally arranged, simple; axillary bud often developed into a thorn, apex sharp to rounded; petiole relatively long, basally and apically pulvinate, with longitudinal grooves when dry, hairy; blade ovate, papery, symmetric, base peltate or not, emarginate to rounded, margin shallowly, bluntly dentate, teeth ending in glands, the latter basally more or less grouped and large in the non-peltate leaves, apex acute to acuminate, very apex round, upper surface glabrescent, bases of hairs showing as white dots, lower surface very densely hairy, without glands; venation palmate with secondary nerves ending open near margin, veins scalariform, quaternary veins reticulate. *Inflorescences* terminal racemes, single, seldom branching with very short branches, either staminate, pistillate or mixed with the basal flowers pistillate; rachis and pedicels somewhat longitudinally grooved when dry, densely hairy. *Bracts* linear, completely hairy. *Flowers* actinomorphic; pedicels with basal abscission zone. *Staminate flowers*: sepals 5, ovate to elliptic, valvate, outside densely hairy, inside glabrous; petals 5, elliptic, longer than sepals, membranous, glabrous, apex frayed, nerves many, parallel; stamens 110–130, free, on convex, stellately hairy receptacle, filaments thread-like, glabrous, anthers basidorsifixed, 2-locular, opening latrorse? with lengthwise slits; disc absent; pistillode absent. *Pistillate flowers*: sepals 5 or 6, ovate, imbricate?, densely hairy, inside mainly simple hairs; petals absent; disc annular, flat, glabrous; pistil 3- (or 4-)locular, one ovule per locule, smooth, tomentose; style short, hairy, stigmas entire, below hairy, above with long slender fimbriae. *Fruits* slightly lobed capsules, triangular in transverse section, septicidal from apex to base, loculicidal from base to apex, outside densely tomentose, inside glabrous except for a few hairs at the base, somewhat woody, thin-walled; column slender, apically not broadened to basally and

apically broadened, hardly any remnants of the septa; septa with a single apical and basal vein. *Seeds* 3 per fruit, very angular and ribbed when immature; covered by a thin, fleshy sarcotesta. *Embryo* not seen.

Distribution — Monotypic, as the species.

***Doryxylon spinosum* Zoll. — Fig. 3, Map 2**

*Doryxylon spinosum* Zoll., Natuurk. Tijdschr. Ned.-Indië 14 (1857) 172; Linnaea 29 (1859) 469; Merr., Sp. Blancoan. (1918) 221; Enum. Philipp. fl. Pl. 2 (1923) 427; Airy Shaw, Kew Bull. 37 (1982) 16; Alph. Enum. Euphorb. Philipp. Is. (1983) 21. — *Sumbavia rottleroides* Baill., Etude Euphorb. (1858) 390, nom. superfl.; Müll. Arg. in DC., Prodr. 15, 2 (1866) 728; Fern.-Vill., Nov. App. (1880) 193; S. Vidal, Phan. Cuming. Philipp. (1885) 143; Revis. Pl. Vasc. Filip. (1886) 243; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 285; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vi (1912) 12, f. 2: A–D; Merr., Fl. Manila (1912) 291. — Type: *Zollinger 3341* (holo P; iso L), Indonesia, Lesser Sunda Islands, Sumbawa, Bima.

*Adelia acidoton* Blanco, Fl. Filip. (1837) 815, non L.; Fl. Filip., ed. 2 (1845) 562; Fl. Filip., ed. 3, 3 (1879) 226, t. 463. — Neotype (proposed here): *Merrill Species Blancoanae 933* (holo L; iso NY), Philippines, Luzon, Rizal Prov.

[*Mercadao mandalojonensis* Náves in Blanco, Fl. Filip., ed. 3 (1877–1883) t. 463, nom. nud.]

(Small shrub to) tree, up to 15 m high, dbh up to 25 cm; flowering twigs 2–3 mm thick. Outer *bark* smooth to rough to sharply fissured, corky, (light) brown (to grey), c. 3 mm thick; inner bark (pale) brown to yellowish whitish or pale brown inside, fleshy, c. 1 cm thick; wood dirty white. *Stipules* 0.6–1.3 by 0.3–0.5 mm. *Leaves*: thorns up to 11 mm long; petiole 0.7–11 cm long; blade ovate, 2.8–12 by 2.2–12 cm, index 1–1.3, base up to 3(–7) mm peltate, dull dark green above, white to grey beneath, venation impressed above, raised below, nerves 5 or 6 per side. *Inflorescences* up to 10 cm long. *Bracts* 5.8–9.5 by 0.6–0.8 mm. *Staminate flowers* c. 14 mm diam.; pedicel 3.2–3.8 mm long; sepals 5.8–7.5 by 2.2–3.5 mm; petals 6.2–8.3 by 2.7–3.5 mm, white; stamens: filaments c. 3.2 mm long, anthers c. 1.2 by 0.5 mm; receptacle c. 0.5 mm high. *Pistillate flowers* c. 7.5 mm diam.; pedicel c. 4.2(–10.5 in fruit) mm long; sepals 4–6.7 by 1–2 mm; ovary ovoid, 3–6 by 3.5–5.5 mm wide; style 1–2 mm long, stigmas spreading, up to 2 mm long, apices recurved. *Fruits* 10–14 by 5–8 mm, brown; column c. 5.5 by 1 mm. *Seeds* 4–5 mm diam.

Distribution — Malesia: disjunct in the Philippines (Luzon) and the Lesser Sunda Islands (Bali, Sumbawa, Flores).

Ecology & Habitat — Commonly found in dry areas with a yearly dry monsoon: open places, savannah with trees, monsoon forest (with *Schleichera*, *Schoutenia*, *Tectona*, *Protium*, and *Tamarindus*), ridges; also along roads and near villages. Soil or bed rock: calcareous, sand breccias, tuff. Altitude: sea level up to 275 m. Flowering: April–June (Philippines), June–December (Lesser Sunda Islands); fruiting: May–July (Philippines), December–May (Lesser Sunda Islands).

Vernacular names — Philippines: Aliparo, dilap, kilap, kirap (Tagalog); balintauak, malabuauan (Pampangan); kim-mo (Iloko) (Merrill, 1923). Lesser Sunda Islands, Flores: Bebang; Sumbawa: Kaju kali bemang, kaju wamba (Zollinger, 1857).

Uses — Noted to be of possible ornamental value.

Notes — 1. The material only contained staminate flowers in bud or flowers which were just opening, therefore, a possible raised receptacle (torus) could not be observed. Also, only older pistillate flowers were present and no mature fruits.

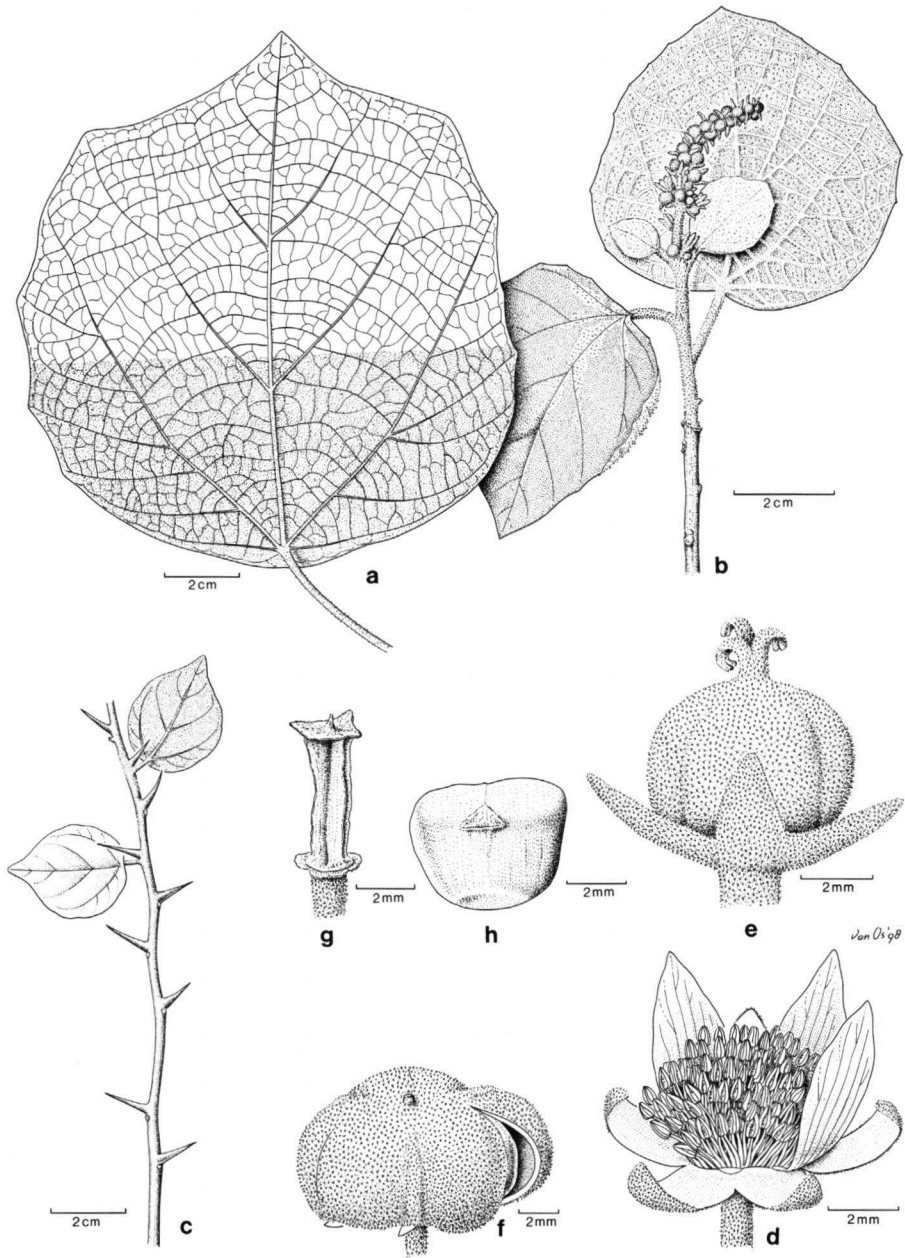
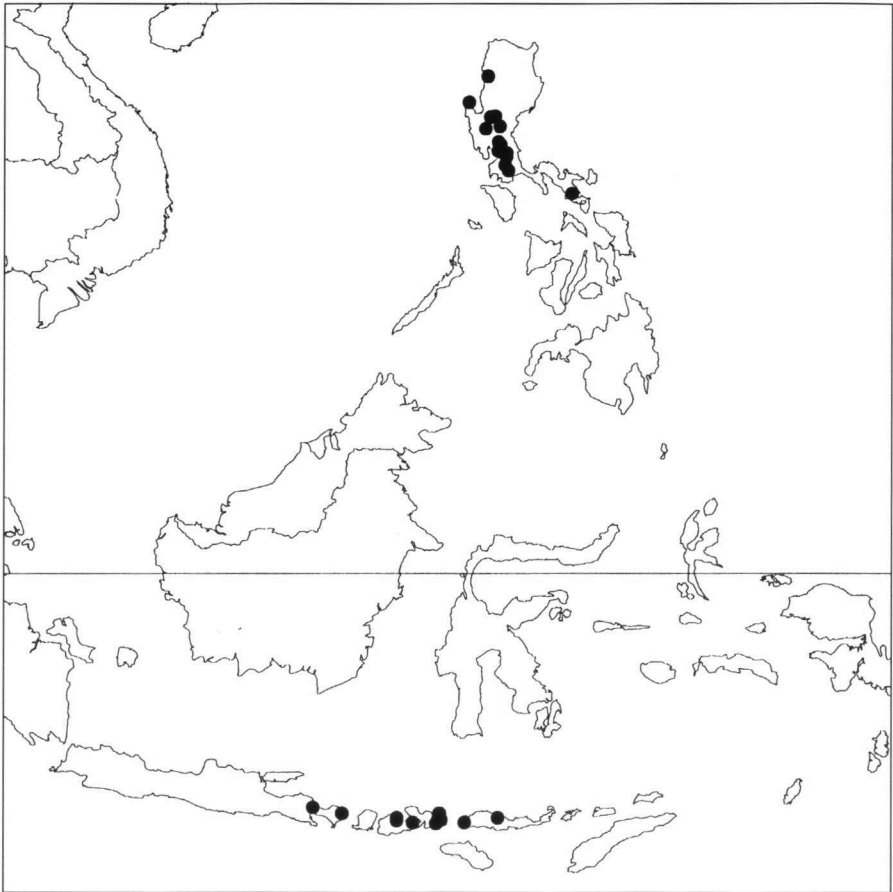


Fig. 3. *Doryxylon spinosum* Zoll. a. Peltate leaf; b. habit showing non-peltate leaves and male buds; c. branchlet with thorns (axillary buds); d. staminate flower; e. pistillate flower; f. fruit; g. fruit column after dehiscence; h. seed [a, c: *M.S. Clemens 18149*, UC; b: *Schmutz 1710*, L; d: *Merrill Species Blancoanae 933*, NY; e–h: *Verheijen 2617*, L].



Map 2. Distribution of *Doryzylon spinosum* Zoll.

2. The material from the Lesser Sunda Islands is only in minor details different from the Philippine specimens. Lesser Sunda Islands: leaves seldom peltate, glands along leaf margin larger, and basally (due to absence of peltation) often grouped as in the genus *Melanolepis*, the indumentum tends to be browner when dry, especially on the flowers.

### SUMBAVIOPSIS

*Sumbaviopsis* is a monotypic genus established by Smith (1910). Its single species, *S. albicans* was first described by Blume (1825) and provisionally placed in the genus *Adisca*. After its first publication it has been classified in several different genera (*Rottlera*, *Croton*, and *Cephalocroton*) until Smith (1910) described it under *Sumbaviopsis*. It was independently described by Müller Argoviensis as *Sumbavia macrophylla* (another commonly used name; 1864) and as *Coelodiscus speciosus* (1865).



A problem in the study of *Sumbaviopsis* is the fact that very few specimens with mature staminate or pistillate flowers were collected. Therefore, a very strange character of *Sumbaviopsis* has remained hidden up to now. The stamens seem to be implanted on a raised receptacle. It is probably a receptacle (or torus) and not an androphore of united filaments as it is of a very different structure than the filaments. It is clavate, with the peduncle glabrous and longitudinally ribbed and the club-like apex covered with stellate hairs. The height of this torus is variable, it is hardly present in Thailand, somewhat longer in Sumatra, and longest in Borneo. Other typical characters for *Sumbaviopsis* are the petioles, inflorescences, and pedicels with longitudinal grooves when dry, the stellate indumentum, the stems with a broad soft pith, the large, mainly ovate leaves which can be dentate, the yellow abaxial glands near the base and margins of the blade, the stellate indumentum, the presence of petals in staminate flowers, the many free stamens, the absence of a disc, 3-colporate heterobrochate pollen, the imbricate pistillate sepals, the 2- or 3-locular ovaries, the short style and split stigmas, the lobed, brown capsules, the column of which has a very broad flat apex, the seed with a sarcotesta. The species is presumably monoecious, though usually only flowers of one sex are found per specimen. Occasionally specimens with both sexes present on separate inflorescences are found and then always some with fruits and others with buds of staminate flowers as if the sexes appear at different times.

The species is somewhat variable, not only in the torus, but also in the leaves, which can be (sub)entire to dentate. The fruits are usually lobed, but not so in Borneo, where they are larger and unlobed.

### **Sumbaviopsis J.J. Sm.**

*Sumbaviopsis* J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 356; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vi (1912) 13; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1925) 418; Backer & Bakh.f., Fl. Java 1 (1964) 477; Airy Shaw, Kew Bull. 26 (1972) 341; Whitmore, Tree Fl. Malaya 2 (1973) 132; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 197; Kew Bull. 36 (1981) 346; Alph. Enum. Euphorb. Philipp. Is. (1983) 45; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 73.  
— Type species: *Sumbaviopsis albicans* (Blume) J.J. Sm.

(Shrub to) tree, monoecious, but usually only one sex per plant; flowering twigs smooth, very shortly tomentose, with a broad soft pith. *Indumentum* consisting of stellate hairs and probably simple ones, latter indistinct. *Stipules* triangular, densely hairy outside except for the probably glandular apex, glabrous inside, early caducous, scars very indistinct. *Leaves* spirally arranged, simple; petiole relatively long, basally and apically pulvinate, with longitudinal grooves when dry, hairy; blade ovate (to elliptic), papery, symmetric, base peltate, rounded, margin (sub)entire to dentate, with few glands along the margin or on the apex of teeth, apex acuminate to cuspidate, very apex acute, upper surface glabrescent, lower surface very densely hairy, with many dark yellow round glands near the base and along the margins near the nerves; venation pinnate with secondary nerves indistinctly looped and connected near margin, veins scalariform, quaternary veins reticulate. *Inflorescences* terminal or (pseudo)axillary (see note), pendulous, thyrsoid when staminate, raceme-like when pistillate, single or 2 together, not (or hardly) branching, either with only staminate or pistillate flowers, fruits often only developed at base, then perhaps upper flowers staminate; staminate flowers up to 3 per cymule, pistillate flowers one per cymule; rachis and pedicels

with longitudinal grooves when dry, densely hairy. *Bracts* ovate, outside hairy, inside glabrous. *Flowers* actinomorphic; pedicels with basal abscission zone; disc absent. *Staminate flowers*: sepals 3–5, ovate, valvate, outside densely hairy, inside glabrous; petals 4 or 5,  $\pm$  ovate, much shorter than sepals, membranous, glabrous, apex irregularly truncate; stamens c. 75, free, on a torus, torus wall with longitudinal ribs, apex broadened, convex, with stellate hairs, filaments thread-like, glabrous, anthers basidorsifixed, 2-locular, opening introrse with lengthwise slits; pistillode absent. *Pistillate flowers*: sepals 5 (or 6), ovate, imbricate, outside densely hairy, inside glabrous; petals absent; pistil 2- or 3-locular, one ovule per locule, smooth, tomentose; style short, hairy, stigmas apically lobed, below hairy, above with long slender fimbriae, especially on the lobed parts. *Fruits* lobed capsules (or not on Borneo), septicidal, later (only apically at first) also loculicidal, outside densely floccose, inside glabrous except for a few hairs at the base, somewhat woody, thin-walled; column with a very large, broadened apex, with hardly any remnants of the septa; septa with a single vein. *Seeds* usually 2 or 3 per fruit, almost globose except for flat area at attachment; covered by a thin, fleshy sarcotesta; exotesta thin, smooth, mesotesta woody, endotesta fibrous. *Embryo* straight, with flat cotyledons, endosperm copious.

Distribution — Monotypic genus, distribution as the species.

Note — The growth is presumably in flushes, including the inflorescence. When young the inflorescence is terminal and it has a few side-branches. Below the side-branches, normal leaves develop and then the side-branches will appear as axillary inflorescences next to the terminal and pseudo-axillary inflorescence. The latter are infructescences next to which side-branches have developed through sympodial growth, the infructescences are then opposite to the leaves.

### **Sumbaviopsis albicans** (Blume) J.J. Sm. — Fig. 4, Map 3

*Sumbaviopsis albicans* (Blume) J.J. Sm., Meded. Dept. Landb. Ned.-Indië 10 (1910) 357; Elmer, Leaflet Philipp. Bot. 4 (1911) 1304; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vi (1912) 14; IV.147.vii (1914) 424; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 428; Gagnep. in Lecomte, Fl. Indo-Chine 5 (1925) 418, f. 49: 13–18; Merr., Pl. Elmer. Born. (1929) 156; Airy Shaw, Kew Bull. 14 (1960) 357; Backer & Bakh.f., Fl. Java 1 (1964) 477; Airy Shaw, Kew Bull. 26 (1972) 341; Whitmore, Tree Fl. Malaya 2 (1973) 132; Airy Shaw, Kew Bull. Add. Ser. 4 (1975) 197; Kew Bull. 36 (1981) 346; Alph. Enum. Euphorb. Philipp. Is. (1983) 45. — *Adisca* ? *albicans* Blume, Bijdr. (1826) 611. — *Rottlera* ? *albicans* (Blume) Hassk., Cat. Hort. Bot. Bogor. (1844) 238, excl. description in note 2. — *Croton albicans* (Blume) Moritz ex Rchb.f. & Zoll., Acta Soc. Regiae Sci. Indo-Neerl. 1 (1856) 21; Linnaea 28 (1856) 322; Boerl., Handl. Fl. Ned. Ind. 3, 1 (1900) 283. — *Cephalocroton* ? *albicans* (Blume) Müll. Arg., Linnaea 34 (1865) 760; Scheff., Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 120. — *Doryxylon albicans* (Blume) N.P. Balakr., Bull. Bot. Surv. India 9 (1967) 58, f. 1–7. — Type: *Anonymous s.n.* (holo L, barcode L 0023770), Java, Prov. Tjanjor.

*Sumbavia macrophylla* Müll. Arg., Flora 47 (1864) 482; in DC., Prodr. 15, 2 (1866) 727; Hook.f., Fl. Brit. India 5 (1887) 408; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vi (1912) 12, f. 2E. — Type: *Griffith KD 4791* (holo K; iso CAL; photo L), Myanmar.

*Coelodiscus speciosus* Müll. Arg., Linnaea 34 (1865) 154; in DC., Prodr. 15, 2 (1866) 760; Hook.f., Fl. Brit. India 5 (1887) 426. — *Mallotus speciosus* (Müll. Arg.) Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.vii (1914) 205. — Type: *Hb. Lenormand* (holo P?, n.v.), India Orientalis.

*Sumbaviopsis albicans* (Blume) J.J. Sm. var. *disperma* Gagnep. in Lecomte, Fl. Indo-Chine 5 (1925) 420. — Type: *Poilane 10741* (holo P; iso UC), Annam, Prov. de Quang-tri, Lang-khoai.

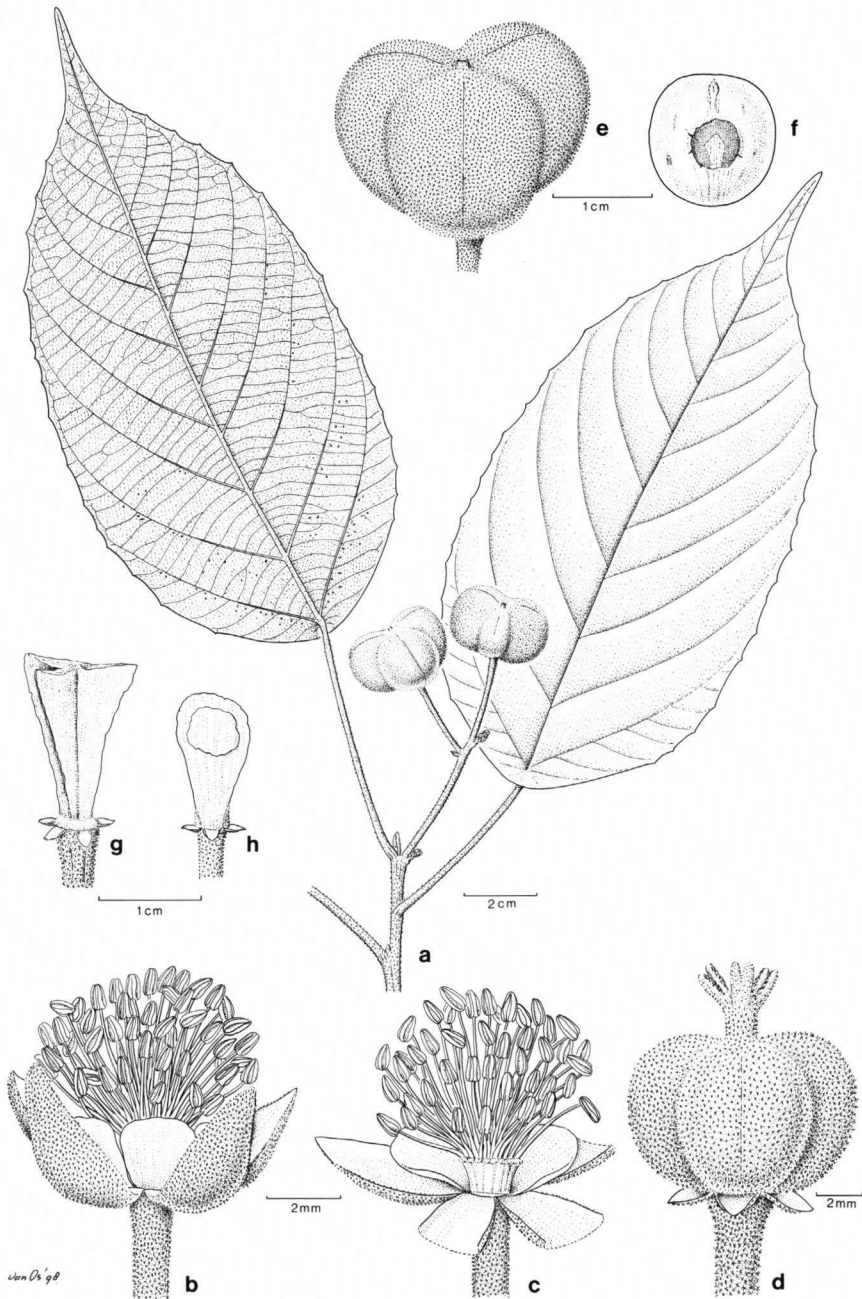
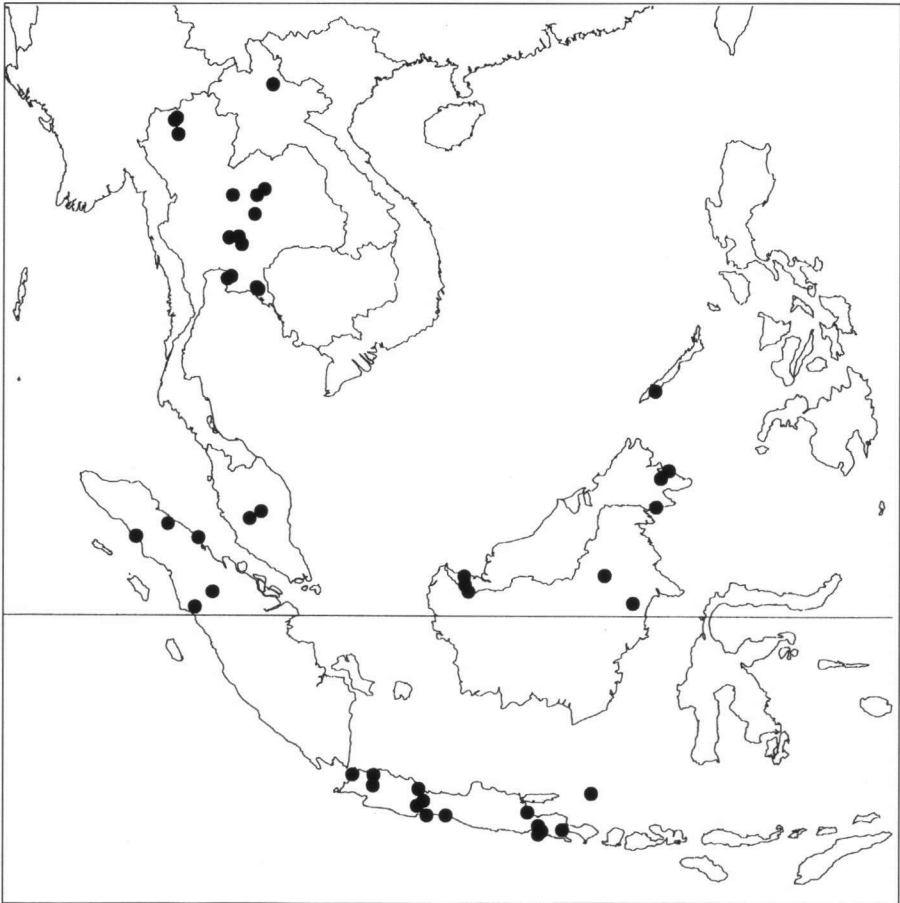


Fig. 4. *Sumbaviopsis albicans* (Blume) J.J. Sm. a. Habit; b. staminate flower; c. staminate flower with a few of the sepals and petals removed, note torus; d. pistillate flower; e. fruit; f. seed; g. column of 3-locular fruit after dehisence; h. column of 2-locular fruit after dehisence [a, e: Geesink, Hattink & Phengkhiai 6702; b, c, g: De Wilde & De Wilde-Duyffes 20048; d: Maxwell 75-177; f, h: Larsen, Santisuk & Warncke 2990; all L].

(Shrub to) tree up to 27 m high, dbh up to 20 cm; buttresses absent; flowering twigs 3–5 mm thick, light brown, hairy; young ones white. Outer bark (light) brown to blackish green mottled with whitish green, smooth to scaly; inner bark brown; cambium brown; sapwood white to yellowish brown. *Stipules* c. 0.6 by 0.4 mm. *Leaves*: petiole 1.2–11.2 cm long, white; blade ovate (to elliptic), 6.8–37 by 3.2–19 cm, index 1.6–2.6, smooth, peltate by 2–8 mm, dull light to dark green above, greyish white beneath, venation impressed above, raised below, nerves 10–12 per side. *Inflorescences* grey whitish; pedicels white; buds pale brown; staminate ones up to 16 cm long, pistillate ones up to 38 cm long. *Bracts* c. 2 by 1 mm. *Staminate flowers* 8–11 mm diam.; pedicel c. 2.2 mm long; sepals 4.2–5.8 by 2–3.2 mm, brown; petals 1.7–2.8 by 1.7–2.5 mm, pale green; stamens: filaments 2.5–2.8 mm long, white, anthers 1–1.1 by 0.4–0.6 mm, white to yellow; torus up to 1.4 mm high. *Pistillate flowers* c. 3.3 mm diam.; pedicel 2.8–3.5 (–4.2 in fruit) mm long; sepals 2.3–4 by 1.5–2.5 mm; ovary 2.7–4.5



Map 3. Distribution of *Sumbaviopsis albicans* (Blume) J.J. Sm.

by 2.7–3.5 mm wide; style 0.8–1.6 mm long, stigmas spreading, up to 3 mm long with up to the last 1 mm split. *Fruits* 2.1–3.6 by 1.4–3 cm, bright to dark brown, tomentum light brown; possessing white latex; column 9–25 by 5–13 mm. *Seeds* 12–20 by 12–15 mm, black; hilum 1.2–2.2 by 2–4 mm. *Embryo* too young to measure; cotyledons white.

Distribution — India (Assam, Naga Land, Tripura), Myanmar, Thailand, Vietnam, and Malesia: Peninsular Malaysia, Sumatra (Aceh, Sumatera Utara), Java, Borneo (Kalimantan Timur, Sabah, Sarawak), and the Philippines (Palawan).

Ecology & Habitat — Scattered to locally common in primary mixed Dipterocarp forest, gallery forest, dry and/or mixed evergreen forest, secondary forest; in the forest (even with heavy undergrowth), at margins of forest, in open places, along ridges and along streams. Terrain level to hilly. Soil (may be thin) and bedrock: limestone, shale, sandstone, yellow-red loam. Altitude sea level up to 800 m. Flowering and fruiting more or less the whole year through.

Uses — The seeds are edible.

Vernacular names — Thailand: Pang tua phu. Vietnam: A luan ray mang (Gagnepain, 1925). Sumatra: Sempaling (Karo-land). Java: Walih angin. Borneo: Kalimantan: Buantik; Sarawak: Brati (Land Dayak); mantas (Iban). Philippines: Dabdab-balod (Tagbanu) (Elmer, 1911).

## THYRSANTHERA

*Thyrsanthera* was established by Gagnepain (1924, 1925) based on a manuscript by Pierre. It is a monotypic genus, with the single species *Th. suborbicularis*. It is a rare plant, a small tree, but mainly collected as a woody shrub or herb-like shrub. The latter is probably due to the fact that the plant is regularly burnt, which results in short parts above the ground and an unexpectedly large root system under the ground. The visible parts are consumed by fire, while the root system survives and produces new shoots. According to Airy Shaw (1965), the plant is a coloniser of waste ground (which is usually burnt regularly).

Typical characters (see also Webster, 1994) are the dense stellate indumentum, almost present everywhere; the usually orbicular, simple, alternate leaves with glands at the lower surface and absence of basal laminar glands; the terminal racemes with basally pistillate and apically staminate flowers; the valvate sepals; petals in the staminate flowers only; presence of a disc in both types of flowers; the 40–60 united stamens; the 3-colporate, heterobrochate pollen grains; the 3-locular ovary with split or unlobed stigmas; the septicidally splitting capsule; and the angular, obovoid, small seeds with translucent, thin sarcotesta.

### *Thyrsanthera* Pierre ex Gagnep.

*Thyrsanthera* Pierre ex Gagnep., Bull. Soc. Bot. France 71 (1924) 878; in Lecomte, Fl. Indo-Chine 5 (1925) 299; Pax & K. Hoffm. in Engl. & Harms, Natürl. Pflanzenfam. ed. 2, 19c (1931) 90; Airy Shaw, Kew Bull. 19 (1965) 308; Kew Bull. 26 (1972) 343; G.L. Webster, Ann. Missouri Bot. Gard. 81 (1994) 75. — Type species: *Thyrsanthera suborbicularis* Pierre ex Gagnep.

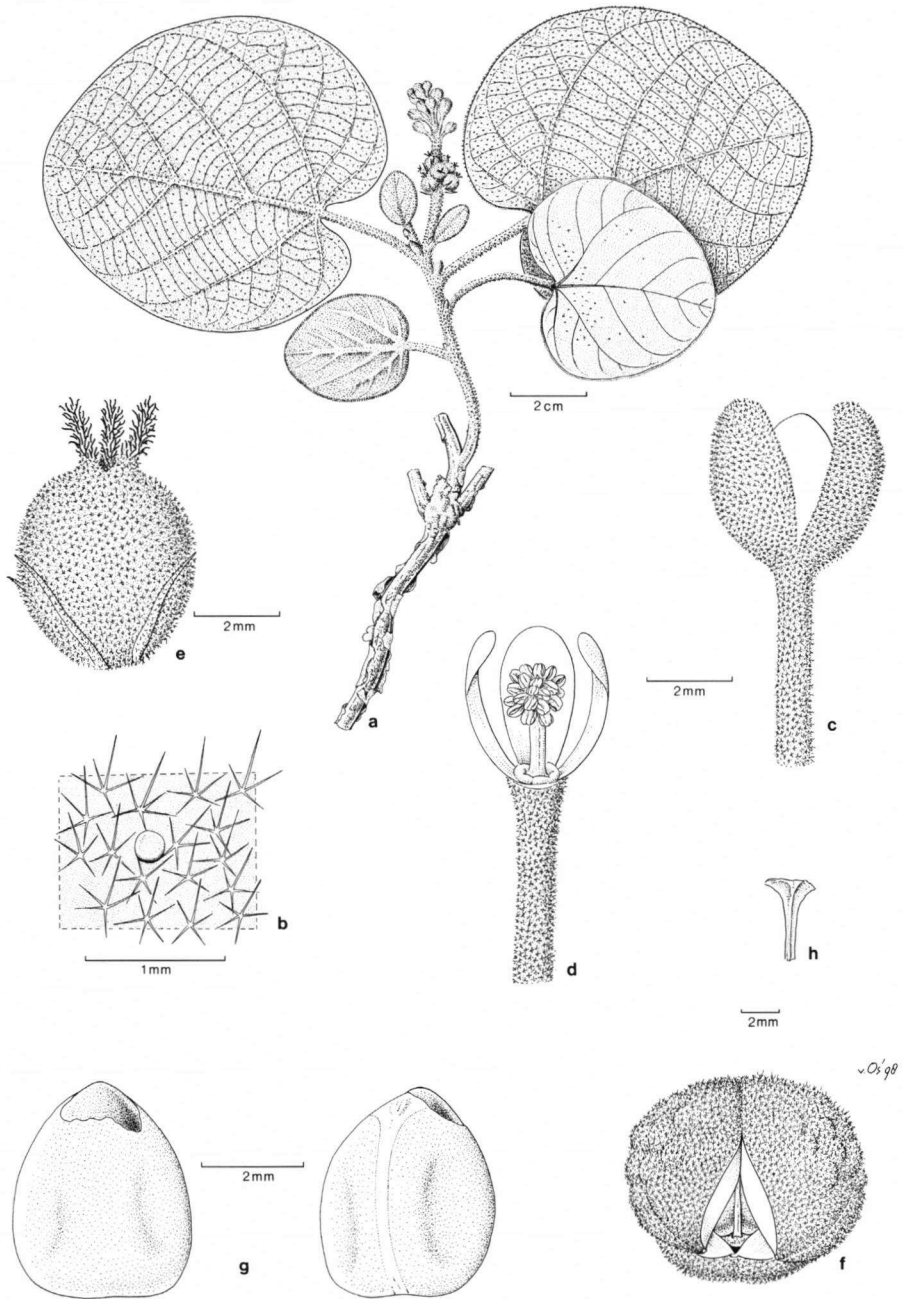
Herb-like shrub to tree, monoecious; flowering twigs ribbed when dry, tomentose, especially when young. *Indumentum* consisting of very dense, sessile and stalked stellate hairs. *Stipules* narrowly triangular, tomentose, caducous, scars very indistinct. *Leaves* spirally arranged, simple; petiole relatively long, not pulvinate, dorsiventrally flattened, longitudinally grooved and tortuous when dry, tomentose; blade ovately orbicular to ovate, coriaceous, symmetric, base emarginate (to truncate), with a rim along the attachment with the petiole, margin entire to shallowly crenate, apex rounded (to acute and mucronulate), upper surface strongly glabrescent, bases of hairs showing as white dots, lower surface tomentose, with subsessile glands, club-shaped, apex hollow, either small and scattered or large (c. 1 mm diam.) and in a more or less submarginal row; venation palmate with at least 5 distinct basal nerves, pinnate along midrib with nerves looped and joined near margin, veins scalariform, quaternary veins reticulate. *Inflorescences* terminal racemes (pseudo-lateral in fruit due to extension of axillary buds), single, not branching, basal flowers pistillate, apical ones staminate; rachis tomentose. *Bracts* narrowly triangular, completely hairy. *Flowers* actinomorphic, one per bract, alternate; pedicels with basal abscission zone; sepals 5, valvate, tomentose outside, glabrous inside; disc annular and lobed or divided into 5 separate glands, glabrous. *Staminate flowers* subsessile to pedicellate; sepals ovately elliptic, 3-veined; petals 5 (or 6), obovate, shorter to slightly longer than sepals, valvate, membranous, pilose with stellate and simple hairs, apex slightly emarginate to rounded; stamens 40–60, glabrous, filaments united into a column, free part thread-like, anthers basifixed, 2-locular, opening laterose with lengthwise slits; annular or consisting of separate lobes; pistillode absent. *Pistillate flowers* sessile to subsessile; sepals linear; petals absent; disc annular; pistil 3-locular, one ovule per locule, smooth, tomentose; style short, hairy, stigmas lobed or not, below hairy, above with long slender papillae. *Fruits* slightly lobed capsules, triangular in transverse section, dehiscent septicidally into 3 bivalved parts, outside densely tomentose, inside glabrous, thin-walled; column slender, without remnants of the septa, apically triangular; septa single veined?. *Seeds* 3 per fruit, obovoid, angular; covered by a thin, translucent sarcotesta. *Embryo* not seen.

Distribution — Monotypic genus, distribution as the species.

***Thyrsanthera suborbicularis* Pierre ex Gagnep. — Fig. 5, Map 4**

*Thyrsanthera suborbicularis* Pierre ex Gagnep., Bull. Soc. Bot. France 71 (1924) 878; in Lecomte, Fl. Indo-Chine 5 (1925) 299, f. 32: 2–6; f. 33 1, 2, 2'; Airy Shaw, Kew Bull. 19 (1965) 308; Kew Bull. 26 (1972) 343. — Lectotype (proposed here): *Pierre 512* (P), Kampuchea (Cambodia), Pen-lover.

Herb-like shrub to tree, 20 cm up to 2(–20?) m high; flowering twigs 2–4 mm thick. *Stipules* c. 2.3 by 0.4 mm. *Leaves*: petiole 2.8–6 cm long; blade 3.8–17 by 3.2–15 cm, index 0.9–1.3, venation impressed above, raised below, nerves 3–5 per side. *Inflorescences* up to 6(–16) cm long. *Bracts* very inconspicuous to c. 5.5 by 1 mm. *Staminate flowers* 4.5–9 mm diam., light yellow; pedicel 2.2–4.5 mm long; sepals 4–4.5 by 1.2–1.6 mm, apex bent inwards; petals 3.2–5.5 by 1.2–2.1 mm, androphore 3.3–3.5 mm long, lower 1.5–3 mm without filaments; filaments short; anthers 0.3–0.5 by 0.3–0.5 mm, yellow. *Pistillate flowers* 5–7 mm diam.; pedicel 0–2 mm long; sepals 3.3–6.3 by c. 0.2 mm; ovary ovoid, 5–7 by 3–5.5 mm wide; style 0.9–1.8 mm long,



**Fig. 5.** *Thysanthera suborbicularis* Pierre ex Gagnep. a. Habit; b. detail of lower leaf surface with stellate hairs and raised glands; c. staminate flower, just before anthesis; d. staminate flower (sepals and part of petals removed); e. pistillate flower, sepals bract-like; f. fruit starting to dehisce basally; g. seed from different sides, apex below, with sarcotesta; h. column of fruit after dehiscence [a–d: Maxwell 75-115, L; e: Couderc s. n., P; f–h: Thorel 2014, P].

stigmas erect, up to 4 mm long, apically split for 0–2 mm. *Fruits* c. 10 by 7 mm; column 4–4.5 mm long. *Seeds* 4.2–4.5 by 3.8–4 mm diam.

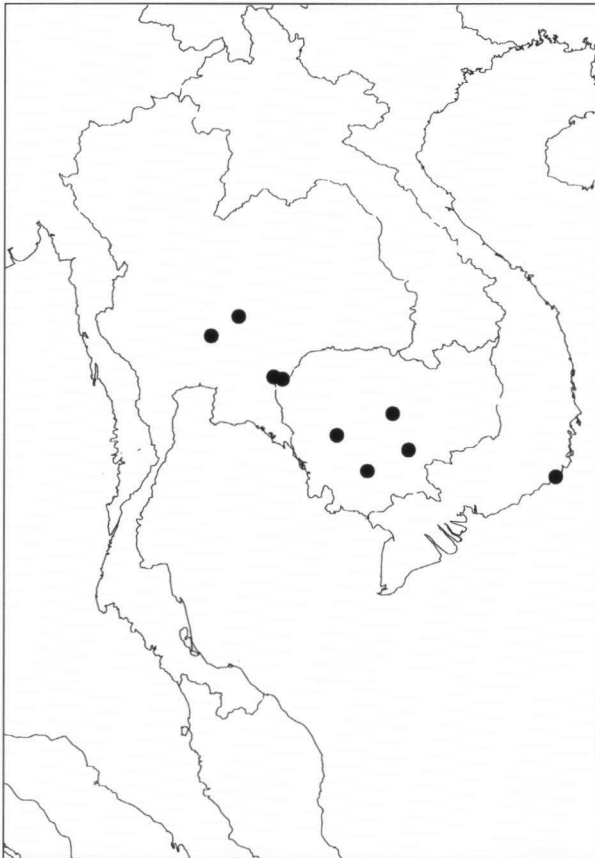
**Distribution** — Thailand, Kampuchea, and Vietnam.

**Ecology & Habitat** — Roadside, waste land, open, rocky-sandy areas, thickets, secondary bush. Altitude 50–100 m. Flowering and fruiting throughout the year, but mainly around August. Probably fire-resistant (short plant above ground, more elaborate and thicker root system underground; see also Airy Shaw, 1965), and coloniser of waste ground.

**Uses** — Used as injection or during washing by women giving birth (Gagnepain, 1925).

**Vernacular names** — Indochina: Baavo, phun tau (Gagnepain, 1925).

**Note** — A somewhat variable species in Vietnam: the glands on the lower leaf surface are much larger and situated in a submarginal row, while in the remainder of the distribution area the glands are much smaller and scattered all over the leaf. In Thailand, one specimen had distinctly pedicellate staminate and pistillate flowers (*Maxwell 75-115*), while all other specimens have mainly sessile staminate and sessile pistillate flowers.



Map 4. Distribution of *Thyrsanthera suborbicularis* Pierre ex Gagnep.



## ACKNOWLEDGEMENTS

I thank the directors of A, AAU, BISH, BM, BO, C, HBG, K, L, MEL, MO, NSW, NY, P, U, UC, and W for use and loans of their collection.

## REFERENCES

- Airy Shaw, H.K. 1965. Notes on Malaysian and other Asiatic Euphorbiaceae. LI. *Thyrsanthera Pierre ex Gagnep.* in Siam. Kew Bull. 19: 308, 309.
- Baillon, M.H. 1858. Étude Générale du groupe des Euphorbiacées: 390. Victor Masson, Paris.
- Balakrishnan, N.P. 1967. Studies in Indian Euphorbiaceae – II. The genus *Doryxylon* Zoll. Bull. Bot. Surv. India 9: 56–58.
- Blanco, M. 1837. Flora de Filipinas: 815. D. Candido Lopez, Manila.
- Blume, C.L. 1825. Bijdragen tot de Flora van Nederlandsch Indië: 611. Lands Drukkerij, Batavia.
- Bremer, K. 1988. The limits of amino acid sequence data in Angiosperm phylogenetic reconstruction. *Evolution* 42: 795–803.
- Elmer, A.D.E. 1911. Euphorbiaceae collected on Palawan Island. *Leafl. Philipp. Bot.* 4: 1304.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Felsenstein, J. & H. Kishino. 1993. Is there something wrong with the bootstrap on phylogenies? A reply to Hillis and Bull. *Syst. Biol.* 42: 193–200.
- Gagnepain, F. 1924. Quelques genres nouveaux d'Euphorbiacées. *Bull. Soc. Bot. France* 71: 878, 879.
- Gagnepain, F. 1925. *Thyrsanthera*. In: M.H. Lecomte, Flore Générale de l'Indo-Chine 5: 299–302, f. 32: 2–6, f. 33: 1, 2, 2'. Masson et Cie, Paris.
- Hillis, D.M. & J.J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42: 182–192.
- Ingram, J. 1980a. The generic limits of *Argythamnia* (Euphorbiaceae) defined. *Gentes Herb.* 11: 427–436.
- Ingram, J. 1980b. A revision of *Argythamnia* subgenus *Chiropetalum* (Euphorbiaceae). *Gentes Herb.* 11: 437–468.
- Linnaeus, C. 1753. *Species Plantarum* 2: 1004. Laurentii Salvii, Holmiae.
- Maddison, W.P. & D.R. Maddison. 1992. *MacClade, Analysis of Phylogeny and Character Evolution, Version 3*. Sinauer Associates Inc., Sunderland.
- Merrill, E.D. 1918. *Species Blancoanae*: 221. Bureau of Printing, Manila.
- Merrill, E.D. 1923. An Enumeration of Philippine Flowering Plants 2: 427. Bureau of Printing, Manila.
- Müller Argoviensis, J. 1864. Neue Euphorbiaceen des Herbarium Hooker in Kew. *Flora* 31: 482.
- Müller Argoviensis, J. 1865. Euphorbiaceae. *Linnaea* 34: 154.
- Náves, A. 1877–1883. In: M. Blanco., *Flora de Filipinas*, ed. 3: t. 463. Plana y Ca., Manila.
- Nelson, G. 1974. Classification as an expression of phylogenetic relationships. *Syst. Zool.* 22: 344–359.
- Prain, D. 1918. VII. – The genus *Chrozophora*. *Bull. Misc. Inform.*: 49–120.
- Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. *Wentia* 7: 1–116.
- Smith, J.J. 1910. Euphorbiaceae. In: S.H. Koorders & Th. Valetton (eds.), *Bijdrage tot de kennis der Boomsoorten op Java* 12. Meded. Dept. Landb. Ned.-Indië 10: 356–360.
- Swofford, D.L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Illinois Natural History Survey, Champaign.
- Van Welzen, P.C. 1998. Phylogenetic versus Linnaean taxonomy, the continuing story. *Taxon* 47: 413–423.
- Van Welzen, P.C., Kartika Ning Tyas, Eviyarni & F.J.M. Gaerlan. 1999. The Malesian species of *Melanolepis* (Euphorbiaceae). *Blumea* 44: 437–446.

Webster, G.L. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Ann. Missouri Bot. Gard.* 88: 33–144.

Zollinger, H. 1857. *Observationes Botanicae Novae*. *Natuurk. Tijdschr. Ned.-Indië* 14: 172.

#### IDENTIFICATION LIST

The numbers after the collectors and their collecting numbers refer to:

- 1 = *Chrozophora rottleri* (Geiseler) A. Juss. ex Spreng.
- 2 = *Doryxylon spinosum* Zoll.
- 3 = *Sumbaviopsis albicans* (Blume) J.J. Sm.
- 4 = *Thyrsanthera suborbicularis* Pierre ex Gagnep.

Ahern's collector 111: 2 — Altmann 542: 1; 548: 1; 549: 1.

Backer 4267: 3; 17825: 3; 18016: 3; 18767: 3; 27559: 3 — Balakrishnan 1000: 1 — Bartlett & LaRue 131: 3 — Becking 55: 2 — Béjaud 822: 4 — Beumée 2741: 3; A767: 3 — Bogor Botanical Garden IX.A.47: 3 — BS series 17845: 2 — Bumisra 335: 1 — Burley & Tukirin et al. 2945: 3 — Buwalda 7248: 3.

Chin 1088: 3 — Chow & Wan 80050: 3 — Clemens 15838: 2; 17296: 2; 18149: 2; 18261: 2 — Clemens & Clemens 20483: 3 — Colfs 142: 2 — Cuming 1404: 2.

De Jong 391: 3 — De Voogd 1638: 2; 1906: 2 — De Wilde & De Wilde-Duyfjes 20048: 3 — Dickason 6994: 1; 7172: 1.

Elbert 3738: 2; 3816: 2; 3910: 2 — Elmer 8187: 2; 12636: 3; 18194: 2; 20970: 3; 21184: 3 — Endert 5213: 3.

FB series 1139: 2; 3165: 2; 8456: 2; 10051: 2.

Gandrup 507: 3 — Geesink, Hattink & Phengkhilai 6702: 3; 6988: 3 — Geesink, Phanichapol & Santisuk 5647: 3 — Godefroy 183: 4 — Griffith KD 4791: 3.

Haenke 586: 2 — Harmand 378: 3.

Jacobs 4782: 3.

Kartawinata 225: 2 — Kerr 5704: 3; 5725: 1; 9781: 4; 19595: 4; 19946: 1 — Kjellberg 967: 3 — Koorders 12815: 3; 27373: 3; 28924: 3; 28928: 3; 30559: 3 — Kostermans 18022: 2; 19018: 3; 19206: 2; 21306: 3; 21432: 3 — Kostermans, Kartawinata, Soegeng & Soepadmo KK+SS 46: 2 — Kostermans & Wirawan 313: 2.

Lakshnakara 1350: 3 — Larsen 10567: 3 — Larsen, Larsen, Nielsen & Santisuk 31546: 3; KL 31877: 4 — Larsen, Santisuk & Warncke 2990: 3; 3294: 3 — Larsen, Smitinand & Warncke 1092: 3 — Loher 4699: 2; 6872: 2 — Lörzing 6345: 3; 6707: 3; 14973: 3.

Marcan 2113: 1 — Martin 20: 4 — Maxwell 71-125: 1; 71-302: 1; 75-115: 4; 75-177: 3; 75-508: 3; 89-430: 3; 89-656: 3 — Merrill 678: 2; 933: 2; 2668: 2; 2857: 2 — Murata, Fukuoka & Phengkhilai T-16342: 3.

Phengkhilai et al. 4219: 3 — Pierre 512: 4; 6570: 4; 6590: 4 — Poilane 131: 4; 5611: 4; 10741: 3; 14537: 4; 20559: 3 — Prawiroatmodjo 476: 3.

Rahayu 346: 3 — Ramlanto Ram 249: 3.

S series 28087: 3; 32620: 3 — SAN series 15043: 3; 35254: 3 — Sangkhachand 1: 3 — Schmutz 821: 2; 1710: 2 — SF series 24526: 3 — Sinclair & Edaño 9446: 2 — Smitinand 8682: 3 — Smitinand & Robbins 7896: 3 — Soejarto, Taylor & Nantasan 5858: 3 — Sørensen, Larsen & Hansen 1920: 1.

Thorel 2014: 4.

Van Beusekom & Santisuk 3263: 3 — Van Steenis 12879: 3 — Vanpruk 292: 3 — Verheijen 2617: 2 — Vidal y Soler 3761: 2.

Wight KD 2613: 1 — Winit 1266: 3; 1700: 3.

Zollinger 3341: 2.