The Erismantheae (monoecious, leaves opposite, stipules interpetiolar) contain three genera, *Moultonianthus* (monotypic), and *Erismanthus* and *Syndyophyllum*, each with 2 species. *Moultonianthus* is recognized by its persistent, large, cordate stipules; *Erismanthus* is characterized by the catkin-like staminate inflorescences with very long-pedicelled flowers; and characteristic for *Syndyophyllum* are the inflorescences with both staminate flowers (in bundles) and pistillate flowers (one per bundle of staminate flowers). Both varieties of *Syndyophyllum occidentale* are now considered to be distinctive species, because an additional difference was found (one axillary bud of each leaf pair present halfway along the petiole or not).

The phylogenetic analysis of the Erismantheae, in comparison with two other tribes in the subfamily Acalyphoideae, the Chaetocarpeae and the Cheiloseae, shows that the Erismantheae are a very distinct, monophyletic group. Within the Erismantheae, *Erismanthus* and *Syndyophyllum* are closest related; all three genera are monophyletic.

**INTRODUCTION**

The tribe Erismantheae is considered to be a natural taxon by Airy Shaw (1975) and Webster (1994); it comprises the genera *Erismanthus*, *Moultonianthus*, and *Syndyophyllum*. Airy Shaw placed the three genera in his informal Crotoneae—Erismanthinae, while Webster classified them in the comparable tribe Erismantheae G.L. Webster of the subfamily Acalyphoideae. *Moultonianthus* is monotypic; *Syndyophyllum* and *Erismanthus* now each contain two species. The Erismantheae are characterized by the opposite leaves with interpetiolar stipules, monoecy, staminate flowers with a torus, 3-locular ovaries with one ovule per locule, lobed, capsular fruits, and seeds without an arilloid. The main differences between the genera are listed in Table 1. Because the opposite leaves with interpetiolar stipules are outstanding in the Euphorbiaceae, the three genera are united.

Not only are the leaves distinctive for this group, but so also the axillary buds. These may be found in very unusual places. Airy Shaw (1960, 1975) considered the opposite leaves, stipules, and buds to be part of a complicated sympodial branching system. Sympodial growth is certainly present, but I think that a horizontal displacement of the meristems is responsible for the position of the axillary buds. *Syndyophyllum occidentale* seems to show a normal situation with the bud in the leaf axil, but in *S. excelsum* one leaf of every pair has the axillary bud halfway along its peti-
Table 1. The differences between the genera of the tribe Erismantheae.

<table>
<thead>
<tr>
<th></th>
<th>Erismanthus</th>
<th>Moultonianthus</th>
<th>Syndyophyllum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Persistent large stipules</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Punctation</td>
<td>present</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Staminate flowers in catkin</td>
<td>present</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Staminate and pistillate flowers</td>
<td>separate</td>
<td>separate</td>
<td>same inflorescence</td>
</tr>
<tr>
<td>on one inflorescence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Petals in staminate flowers</td>
<td>shorter</td>
<td>longer</td>
<td>shorter</td>
</tr>
<tr>
<td>shorter than sepal</td>
<td>than sepal</td>
<td>than sepal</td>
<td>than sepal</td>
</tr>
<tr>
<td>Petals in pistillate flowers</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Stamens</td>
<td>12–15</td>
<td>9–11</td>
<td>4 or 5, 8–10</td>
</tr>
<tr>
<td>Seed with light stripes</td>
<td>present</td>
<td>sometimes</td>
<td>absent</td>
</tr>
<tr>
<td></td>
<td></td>
<td>somewhat</td>
<td></td>
</tr>
</tbody>
</table>

In Moultonianthus the axillary buds appear between the stipules and the leaves. It is likely that the loss of one stipule per leaf and a displacement on the node has caused the different position of buds and stipules. In Erismanthus the situation is most complex. One leaf per node still has an axillary bud, but the other one, alternating with each successive node, lacks the bud. That bud is found in the axil of one of the stipules. There is a complication that one to several very short internodes are also present above the node, which obscure observation. A study of living material is necessary to elucidate fully the secrets of the branching systems in the Erismantheae.

**PHYLOGENY OF THE ERISMANTHEAE**

The genera in the Erismantheae are very distinct and the tribe as a whole seems to be very heterogeneous. Therefore, the monophyletic nature of this group may be disputable. In order to investigate the possible monophyly of the Erismantheae, a preliminary phylogenetic analysis of the tribe Erismantheae in comparison with two other tribes of the subfamily Acalyphoideae, the Chaetocarpeae and the Cheiloseae, was conducted. Eighteen characters (see Table 2) were used in the analysis. The data matrix is shown in Table 3 [data for Cheilosa were obtained from Van Welzen et al. (1993); Neoscoetechinia from Van Welzen (1994a), which also contains a phylogenetic reconstruction of this genus; Chaetocarpus from Van Welzen (1994b); and Trigonopleura from Van Welzen et al. (1995), including phylogenetic notes].

In first instance, a fictitious outgroup was used, with character states common in the Euphorbiaceae. This was done to select genera or species to be used as an outgroup in the final analysis. Cheilosa and Neoscoetechinia appeared to be the first clade to split off in the resulting cladogram after an exhaustive search with PAUP version 3.1.1. (Swofford, 1991). A second analysis with Cheilosa and Neoscoetechinia as outgroup resulted in one cladogram, shown in Figure 1 (length 23 steps, consistency and retention index 1).
Table 2. Characters and character states used in the phylogenetic analysis of the Euphorbiaceae tribe Erismantheae.

<table>
<thead>
<tr>
<th>Character Description</th>
<th>States</th>
<th>State States</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Place axillary buds</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>2. Stipule placement</td>
<td>2</td>
<td>2 = interpetiolar</td>
</tr>
<tr>
<td>3. Stipule persistence</td>
<td>2</td>
<td>2 = long persistent</td>
</tr>
<tr>
<td>4. Leaf placement</td>
<td>2</td>
<td>2 = opposite</td>
</tr>
<tr>
<td>5. Foodbodies in leaf (punctuation)</td>
<td>1</td>
<td>1 = present</td>
</tr>
<tr>
<td>6. Glands at leaf margin</td>
<td>2</td>
<td>2 = at lower side of teeth</td>
</tr>
<tr>
<td>7. Glands at leaf base</td>
<td>2</td>
<td>2 = present</td>
</tr>
<tr>
<td>8. Monoecy or dioecy</td>
<td>2</td>
<td>2 = monocious</td>
</tr>
<tr>
<td>9. Inflorescence type</td>
<td>2</td>
<td>2 = axillary bundles of flowers</td>
</tr>
<tr>
<td>10. Flower type per inflorescence</td>
<td>2</td>
<td>2 = staminate and pistillate flowers</td>
</tr>
<tr>
<td>11. Sepal length</td>
<td>2</td>
<td>2 = more than 7 mm long</td>
</tr>
<tr>
<td>12. Petal presence</td>
<td>1</td>
<td>1 = present</td>
</tr>
<tr>
<td>13. Length pedicel staminate flower</td>
<td>2</td>
<td>2 = more than 1 cm long</td>
</tr>
<tr>
<td>14. Anther placement</td>
<td>3</td>
<td>3 = on androphore</td>
</tr>
<tr>
<td>15. Number of locules</td>
<td>2</td>
<td>2 = 2 locules</td>
</tr>
<tr>
<td>16. Fruit lobes</td>
<td>1</td>
<td>1 = lobed</td>
</tr>
<tr>
<td>17. Fruit wall</td>
<td>2</td>
<td>2 = echinate</td>
</tr>
<tr>
<td>18. Aril</td>
<td>2</td>
<td>2 = completely covering seed</td>
</tr>
</tbody>
</table>

Table 3. The data matrix for the phylogenetic analysis of the Euphorbiaceae tribe Erismantheae. The outgroup is fictitious and based on common characters in the Euphorbiaceae, but this ‘species’ can be left out of the analysis and either Cheilosa or Chaetocarpus can be used as outgroup.

<table>
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<tr>
<th>Taxa</th>
<th>Characters:</th>
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<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
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<tbody>
<tr>
<td>(fictitious outgroup)</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
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<td>1</td>
</tr>
<tr>
<td>Chaetocarpus</td>
<td></td>
<td>1</td>
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<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<td>3</td>
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<tr>
<td>Cheilosa montana (outgroup)</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
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<td>0</td>
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<tr>
<td>Erismanthus obliquus</td>
<td></td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
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<td>2</td>
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</tr>
<tr>
<td>Erismanthus sinensis</td>
<td></td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2</td>
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<tr>
<td>Moultonianthus leembruggianus</td>
<td></td>
<td>2</td>
<td>2</td>
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<td>2</td>
<td>2</td>
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<td>2</td>
<td>1</td>
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<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Neoscoptechinia</td>
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<td>0</td>
<td>2</td>
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<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Syndyophyllum excelsum</td>
<td></td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
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<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Syndyophyllum occidentale</td>
<td></td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
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<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Trigonopleura</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
The analysis shows the Erismantheae to be a distinct, monophyletic group with many synapomorphies. Within the Erismantheae the genera *Syndyophyllum* and *Erismanthus* seem to be closest related (based on the punctation of the leaves).

Figure 1 also shows that all genera and tribes form distinctive monophyletic groups, which can be equated with the levels presently used (tribe and genus), provided the sequence rule is applied (sequence of genera in the classification shows the sequence in which the clades split off; Nelson, 1972). It should be emphasized that in the cladogram the sequence *Cheilosa* / *Neoscortechinia* and *Chaetocarpus* / *Trigonopleura* is not reliable, because this is only based on the fictitious outgroup and can easily be reversed without having any consequence for the length of the cladogram, which remains as parsimonious with *Chaetocarpus* as outgroup. Moreover, the fictitious outgroup is more or less based on the ‘rule’ that common is primitive, which is certainly not always true.

![Cladogram](image)

Fig. 1. The phylogeny of the tribe Erismantheae (genera *Erismanthus*, *Moultonianthus*, and *Syndyophyllum*) in relation to the tribes Chaetocarpeae (*Chaetocarpus* and *Trigonopleura*) and Cheiloseae (*Cheilosa* and *Neoscortechinia*). Delimitation of tribes after Webster (1994).
KEY TO THE GENERA OF THE ERISMANTHAE

1a. Staminate inflorescences thyrses with short-pedicelled flowers (pedicel less than 1.5 cm long). Stamens 4–11. Pistillate inflorescences or mixed inflorescences with several pistillate flowers .................................................... 2
   b. Staminate inflorescences catkin-like with long-pedicelled flowers (pedicel more than 1.5 cm long). Stamens 12–15. Pistillate inflorescences with one flower ..................................................... Erismanthus

2a. Stipules long persistent, ovate, 0.8–4.5 by 0.5–3.6 cm, base cordate. Pedicels of the staminate flowers 2.8–13.3 mm long, of the pistillate flowers and fruits 3–8.2 cm long. Staminate and pistillate flowers in separate inflorescences. Petals longer than sepals .............................................. Moultonianthus
   b. Stipules early caducous, triangular, 3.2–4.9 by 1–1.2 mm, base broad. Pedicels of the staminate flowers less than 1 mm long, of the pistillate flowers and fruits up to 7 mm long. Staminate and pistillate flowers present in the same inflorescences. Petals if present shorter than sepals ...................... Syndyophyllum

ERISMANTHUS

INTRODUCTION

Erismanthus can easily be recognized by its opposite, serrate leaves with oblique cordate base, interpetiolar stipules, two inflorescences per node, one with a single pistillate flower and the other catkin-like with many long-pedicelled staminate flowers, the petals shorter than the sepals, 12–15 stamens, 3-locular ovaries with one ovule per locule, and the lobed, sericeous fruits.

The name Erismanthus was established by Wallich (1846), but no description was given. When Müller Argoviensis provided the description 20 years later (1866), he also formally described the first species, E. obliquus. Oliver (1887) described the second species, E. sinensis, and later on Gagnepain defined a third one (1924), E. indochinensis, which was later shown to be synonymous with E. sinensis (Airy Shaw, 1972).

The two species recognized differ only slightly from each other in the keys presented up to now (E. sinensis usually has smaller, more coriaceous leaves with a somewhat less serrate margin). However, there is another, major difference between both species in the size of the sepals: E. obliquus has much larger sepals than E. sinensis. Other differences are also present, but more difficult to observe (see key). Both species are geographically separated (Map 1), whereby the distribution of E. obliquus is very disjunct.

ERISMANTHUS Wall. ex Müll.Arg.

Shrubs to trees, monoecious, branching sympodially. *Indumentum* consisting of simple, short and long (sub)hirsute hairs, glabrescent. *Stipules* small, interpetiolar, triangular, base broad, margin entire, apex acute, caducous, outside sericeous, inside glabrous. *Axillary buds*: one per node in the axil of a leaf (alternating with each successive node), the other in the axil of a stipule. *Petiole* reniform in transverse section, not pulvinate, hirsute to sericeous. *Leaves* simple, distichous, opposite, symmetric; blade punctate; base oblique, cordate; margin slightly serrate (to crenate), with a gland on each tooth; apex rounded to crenate, very apex emarginate to acute; upper surface pustular with white dots, the latter forming food bodies in young leaves; lower surface smooth; venation pinnate, looped and closed near the margin, triplinerved, above and beneath slightly raised, tertiary veins obliquely subscalariform, quaternary veins reticulate, inconspicuous. *Staminate* and *pistillate inflorescences* separate in same axil of one leaf per pair, alternating per node; staminate ones short, bracteose catkins, per bract one flower; pistillate ones containing a single flower. *Bracts* and *bracteoles* small, triangular to ovate, mainly outside sericeous, bracteoles at base of pedicel of staminate flowers, ± halfway on the pedicel of pistillate flowers. *Pedicels* subhirsute, those of the staminate flowers very long. *Flowers* actinomorphic. *Sepals* 5, imbricate, basally united, glabrous to subhirsute, in staminate flowers membranous, in pistillate flowers bract- or leaf-like. *Petals* shorter than sepals, only in staminate flowers, 5, elliptic to ob-ovate, apex rounded or irregular, membranous, glabrous. *Disc* lobes absent. *Stamens* 12–15, on a short torus, free; filament filiform, glabrous; anther ± triangular, basifixed in deep cleft, opening latrorse by a slit, glabrous; connective without an apical triangular appendix. *Pistil*: ovary 3-locular, hirsute; ovules one per locule, descending, epipetalous, anatropous, attached in upper half of column; style 1, short, hirsute; stigmas 3, apically split into 2 lobes, above papillose, beneath hirsute; in staminate flowers only a bifid or trifid pistillode. *Fruit* a 3-lobed regma, subglobose, outside sericeous, glabrescent, inside glabrous, dehiscing septi- and loculicidally into 6 valves; wall thin, woody, on inside with light short stripes in *E. sinensis*; septum with one splitting vein; columella after dehiscence with a narrow, straight septum margin attached to it, apically broadened. *Seeds* 1–3 per fruit, brown, glossy, micropyle clearly visible, with light brown short longitudinal stripes; arilloid absent. *Embryo* not seen.

Distribution — Two species, one in SE Asia (S China, Laos, Cambodia, Vietnam, N half of Thailand), one in *Malesia*: Penins. S Thailand, Malaysia, Sumatra, Borneo.

Note — The axillary buds are very typical, per node one bud is still found in the axil of a leaf, but the other one is in the axil of one of the stipules.

**KEY TO THE SPECIES OF ERISMANTHUS**

1a. Leaves 7–23 cm long, most leaves on flowering branches more than 10 cm long; apex acuminate to caudate, very apex rounded to acute. Bracts of the staminate flowers 1.6–3 mm long, long acute. Sepals of pistillate flowers 5.5–17 by 3.3–6 mm. Fruit wall inside of one colour .......................... *E. obliquus*

b. Leaves 2.3–13.5(–16.5) cm long, most leaves on flowering branches less than 10 cm long; apex rounded to acuminate (to cuspidate), very apex emarginate to rounded. Bracts of staminate flowers 1.2–1.8 mm long, short acute. Sepals of pistillate flowers 1.3–4.5 by 0.7–2.1 mm. Fruit wall inside with light short stripes  ....  *E. sinensis*
Erismanthus obliquus Wall. ex Müll.Arg. — Fig. 2; Map 1


Tree up to 17 m high, d.b.h. up to 20 cm; girth up to 67 cm; bole fluted; flowering branches 1.2–5 mm thick, smooth, (sub)hirsute when young. Outer _bark_ sandy brown to grey, smooth, thin; inner bark pale brown mottled. _Sapwood_ white. _Leaves:_ stipules 4.3–13 by 1.2–3.3 mm; petiole 1–4 mm long, often reddish when dry; blade elliptic, (7-)10–23 by 2.5–8.2 cm, index 2.3–2.8, chartaceous, margin flat, apex acuminate to caudate, very apex rounded to acute, above and beneath (sub)glabrous, nerves 8–11 per side. _Staminate catkins_ 7–9 by 3.5–4 mm when without flowers, brown; peduncle 1–2 mm long. _Bracts_ of the catkins c. 4.5 by 1 mm; floral bracts c. 1.6–3 by 0.3–0.4 mm, long acute. _Staminate flowers_ c. 2 mm in diam., green to pale yellow brown to cream; pedicel more than 1.5 cm long; sepals elliptic to obovate, 0.9–1.5 by 0.5–0.7 mm; petals 1–1.2 by c. 0.5 mm; stamens 15, filament 0.3–0.6 mm long, anther 0.6–0.9 by 0.4–1 mm; pistillode up to 4.8 mm long. _Pis-

Map 1. Distribution of _Erismanthus obliquus_ Wall. ex Müll.Arg. (dots) and _Erismanthus sinensis_ Oliv. (squares).
tillate flowers c. 2 cm in diam., green to orange-pink; pedicel 2.8–6.5 mm long; sepals leaf-like, ovate, 5.5–17 by 3.3–6 mm, margin slightly serrate, with glands, apex acute, outside and margin subsericeous, inside glabrous; ovary ovoid, 1.2–2 by 1.8–2.5 mm, style 1.2–3.3 mm long, stigmas 1.3–2.4 cm long, upper 1–1.6 cm bifid. Fruits 13–14 mm broad by 8–9 mm high, pale yellow; wall 0.5–0.7 mm thick. Seed ± globose, 4–6 mm in diam.; hilum c. 0.8 mm long. Embryo not seen.

Distribution — Malesia: S Peninsular Thailand, Peninsular Malaysia, N Sumatra (2 specimens), NE and S Kalimantan (2 specimens). See Map 1; the dot in Sumatra only indicates the possible collection site.


Vernacular name — Peninsular Malaysia: Bekoi (Asli).

Erismanthus sinensis Oliv. — Map 1

Erismanthus sinensis Oliv., Hooker’s Icon. Pl. 16 or 6 (1887) 1578; Pax & K. Hoffm. in Engl., Pflanzenr. IV.147.iii (1911) 35; Gagnep. in Lecomte, Fl. Gén. Indo-Chine 5 (1926) 461; Airy Shaw, Kew Bull. 26 (1972) 260. — Lectotype (proposed here): B. C. Henry 23 (K), China, Hainan.


Shrub to tree up to 10 m high, d.b.h. up to 60 cm; flowering branches 1–2.1 mm thick, smooth, hisurate when young. Leaves: stipules: 2.8–8.5 by 0.7–1.6 mm; petiole 1.5–5 mm long, purple when fresh; blade ovate to elliptic, 2.3–10(–16.5) by 0.8–4.7(–6.3) cm, index (2.3–)2.7–4, coriaceous, apex rounded to acuminate (to cuspidate), very apex emarginate to rounded, margin flat to recurved, above glabrous, glossy green, beneath glabrous, duller green, nerves 10–12 per side. Staminate catkins c. 7.5 by 3–4 mm when without flowers, brown; peduncle c. 2.5 mm long. Bracts to the catkins c. 2 by 1 mm; floral bracts 1.2–1.8 by 0.6–1 mm, shortly acute. Staminate flowers c. 2 mm in diam., pinkish to light purple; pedicel 2.5–3 cm long; sepals ovate, c. 1 by 0.7–0.8 mm; petals 0.8–1.4 by 0.5–0.8 mm; stamens 12–15, filament 0.3–0.8 mm long, anther 0.5–1 by 0.3–1 mm; staminode up to 9 mm long. Pistillate flowers c. 1 cm in diam., green; pedicel 1.4–2.6 cm long; sepals

Fig. 2. Erismanthus obliquus Wall. ex Müll. Arg. a. Habit, one but last apical node showing bud in axil of stipule and the other (developed as inflorescence) in the axil of the leaf, × 0.5; b. staminate inflorescence with buds, × 6; c. separate flowering staminate and pistillate inflorescences, latter one-flowered, × 0.5; d. staminate flower with sepals, petals, stamens in two whorls, and pistilode, sepals slightly larger than petals, × 12.5; e. pistillate flower with sepals and pistil, × 12.5; f. dehiscing fruit showing clean and sharp break between septa and column, margin frayed, × 3; g. seed, × 3 [a: Shah MS 1325, L; b–d: Curtis KD 1471, K; e: Kostermans 21118, L; f, g: Argent & Saridan 9341, K].
bract-like, ovate to ligulate, 1.3–4.5 by 0.7–2.1 mm, margin entire, with glands, apex rounded, outside and on margin subsericeous, inside glabrous; ovary ovoid, 2.2–2.8 by 2.3–2.5 mm, style 1.5–2 mm long, stigmas 8.5–9 mm long, upper 6–7.5 mm bifid. Fruits 6.5–13 mm broad by 4.5–7 mm high, wall inside with lighter short stripes; pedicel up to 2.7 cm long; wall c. 0.5 mm thick. Seed 5–6 mm in diam.

Distribution — SE Asia: S China (Hainan Prov.), Laos, Cambodia, Vietnam, and N and Central Thailand. See Map 1.

Habitat & Ecology — Found as tree or undershrub in evergreen forest, often along rivers. Locally common. Soil: granite. Altitude 50–600 m. Male catkins throughout the year; fl. Jan.–Oct.; fr. Jan.–May.

Uses — The wood is of good quality and used for handles of axes and knives (Poilane 10212).

Vernacular namse — Cambodia: Doć, nuon srey, snay nhût.

MOULTONIANTHUS

INTRODUCTION

The genus *Moultonianthus* may readily be recognized by the opposite leaves with serrate margin, the large, persistent interpetiolar stipules, the 2 inflorescences per node with either many bunches of staminate flowers or several single pistillate flowers, the long (especially in pistillate flowers) pedicels, the 5 petals which are longer than the 5 sepals, the 9–11 stamens in 2 whorls, the 3-locular ovary with one ovule per locule and deeply lobed stigmas, and the lobed, tomentose fruits.

The genus *Moultonianthus* was established by Merrill in 1916, and dedicated to the director of the Sarawak Museum, Mr. J.C. Moulton, through whom Merrill obtained rich collections of Bornean plants. Merrill named the only species in this genus *M. borneensis*. Later on Van Steenis (1948) noticed that the species has been described earlier by Boerlage and Koorders (1910) in the genus *Erismanthus*, as *E. leembruggianus* (after one of the herbarium curators in Bogor, then called Buitenzorg, Mr. Leembruggen). The older epithet is *leembruggianus*, and therefore Van Steenis (1948) made the new combination *Moultonianthus leembruggianus*.

MOULTONIANTHUS Merr.


Tree or shrub, monoecious. *Indumentum* consisting of simple hirsute to sericeous hairs (seldom some stellately bundled), very early glabrescent. *Stipules* large, inter

1) With assistance of Katia Hueso and Selvino de Kort, students in Leiden.
petiolar, ovate, base cordate, long persistent. Axillary buds between leaves and stipules. Leaves simple, distichous, opposite; petiole not pulvinate; blade coriaceous, not punctate; base oblique, emarginate to shortly attenuate; margin (sharply) serrate (to crenate), revolute, with a gland on each tooth; apex acuminate to cuspidate, very apex rounded; venation pinnate, looped and closed near the margin, indistinctly reticulate. Inflorescences axillary thyrses, flattened, with either staminate or pistillate flowers, both originating in one axil per leaf pair, alternating per node, subsericeous, glabrescent, purplish, brachyblasts either with short branches and many dichasial bundles of staminate flowers or with single pistillate flowers; staminate inflorescences caducous when pistillate ones fruiting. Bracts ovate to triangular, subsericeous outside. Pedicels purplish, apically broadened, with abscission zone about halfway. Flowers actinomorphic, scented, pistillate flowers opening after pollen release of staminate ones, petals longer than sepal. Sepals 5, imbricate, free, 3 outer smaller, ovate, subsericeous outside, margin ciliate, 2 inner larger, ovate to obovate, glabrous outside, margin papillose; all basally thickened, margins membranous, inside glabrous, (reddish) yellow. Petals 5–7, longer than the sepals, elliptic to obovate, imbricate, margin entire, apex rounded, glabrous, white. Disc-like lobes minute, 5, alternipetalous. Stamens 9–11, on a short torus, free, in 2 whorls, either with short or long filaments; latter filiform, (sub)glabrous, white; anther elliptic, basifixed, opening latrointrorse by a slit, glabrous, chocolate brown; connective with an apical triangular appendage; 1 or 2 staminodes in pistillate flowers. Pistil: ovary 3-locular, densely tomentose, light yellow; ovules one per locule, descending, epipropous, anatropous, attached halfway up the column; style 1, short, hirsute; stigmas 3, white, almost completely divided, lobes flat, broad, above with dendritic papillae, on lower surface hirsute; in staminate flowers pistillode consisting of 3 filiform appendages, glabrous. Fruit a 3-lobed regma, subglobose, outside tomentose, glabrescent, inside glabrous, dehiscing septi- and loculicidally into 6 segments; wall thin, woody. Seeds 1–3 per fruit, brown, sometimes with light brown short longitudinal stripes, glossy, micropyle clearly visible; ariloid absent. Embryo not seen.

Distribution — Monotypic, only found in Malesia: Central Sumatra (only 1 specimen seen) and Borneo (Brunei, Kalimantan, Sabah, Sarawak).

Notes — 1. Airy Shaw (1960, 1975) discussed the opposite leaves with the interpetiolar stipules. He considered the stipules to be transformed leaves, which are decussate with normal leaves. Airy Shaw expected that sympodial growth could explain the nodal situation. The sympodial growth is indeed present besides monopodial growth; often a terminal bud can be found among the leaves and stipules, and an axillary bud has taken over the growth. However, we do consider the stipules to be real stipules, but not only one pair per leaf, but just one stipule per leaf. This reduction is accompanied by a horizontal displacement on the node, whereby the two stipules, one per opposite leaf, became interpetiolar. The displacement is also shown by the axillary buds, as these are not any longer in the axil of the leaf, but they are found between leaf petiole and stipule.

2. Airy Shaw (1960) also described an androphore for Moultonianthus and occasionally bisexual inflorescences (1975). An androphore could not be detected, but the receptacle is heightened into a torus. We did not find any bisexual inflorescences.
Moultonianthus leembruggianus (Boerl. & Koord.) Steenis — Fig. 3, Map 2


(Shrub to) tree, up to 22 m high, d.b.h. up to 40 cm, girth up to 0.75(-1.65) m; stilt roots and buttresses seldom recorded, latter up to 33 cm high, 5 cm thick; flowering branches 1.5–3 mm thick, smooth to slightly ribbed, glabrous (to hirsute, glabrescent). Outer bark grey-brown to red-brown when young, smooth to finely and shallowly fissured, with rectangular flakes, 2–3 mm thick; inner bark yellow to red-brown. Sapwood white; heartwood yellowish. Leaves: stipules 0.8–4.5 by 0.5–3.6 cm, margin entire to sub serrate, apex acute, (sub) glabrous; petiole 4–7 mm long, reniform in transverse section, above often sericeous; blade (ovate to) elliptic (to ovate), 5.5–26.5 by 2.5–11 cm, index 2.6–3.6, glabrous (to subsericeous mainly beneath), lighter green beneath, venation above not raised except for midrib, beneath raised, nerves 10–12 per side. Inflorescences up to 22 cm long. Bracts up to 1.3 by 1 mm. Staminate flowers 5–7 mm in diam.; pedicel 2.8–13.3 mm long, 1.8–11.3 mm long above abscission zone; sepals 1.4–3 by 1.5–2.8 mm; petals 5.3–7.5 by 1.8–2.3 mm; filaments: short ones 0.7–0.8 mm long, long ones 1.7–2 mm long, anthers 0.5–0.8 by 0.5–0.8 mm; appendage on connective up to 0.4 mm long; pistillode 3.5–5 mm long. Pistillate flowers c. 1 cm in diam.; pedicels 3–8.2 cm long, 1.9–5.3 cm long above abscission zone; sepals 2.5–5.5 by 2.9–5 mm; petals up to 15.5 by 6 mm; filament of staminodes: c. 0.5 mm long; anther c. 0.8 by 0.6 mm; ovary 2.8–4.2 by 2.5–5 mm, style c. 1 mm high; stigmas 3.5–4 mm long, lobes 2.5–3 mm long. Fruit 15–18 mm broad by 8–12 mm high, brown; wall c. 1 mm thick; septum with one splitting vein; column after dehiscence with a frayed septum margin attached to it, apically very broadened. Seeds ± globose, 9–10 by 8–10 mm; hilum 2–2.7 mm long. Embryo seen when immature, at least 6 by 6 mm.

Distribution — Malesia: Central Sumatra (one specimen seen: Koorders 22285) and Borneo (Brunei, Kalimantan, Sabah, and Sarawak).


Fig. 3. Moultonianthus leembruggianus (Boerl. & Koord.) Steenis. a. Habit, showing separate inflorescences for staminate and pistillate flowers, × 0.5; b. staminate flower, petals much larger than sepals, × 6; c. staminate flower with sepals and petals removed, showing disc lobes, two whorls of stamens, and pistillode, × 12.5; d. pistillate flower with sepals and petals removed, showing disc lobes and pistil, × 6; e. outline of young fruit, × 3; f. remaining column after fruit dehiscence, × 3; g. seed, × 3 [a: S (Anderson) 20299, L; b, c: SAN (Aban G.) 95168, L; d: Endert 5004, L; e: SAN (Wood) 16526, L; f, g: SAN (Wood & Kapis bin Sisiron) 16836, L].
Vernacular names — Sabah: Ulas (Brunei); ulas bukit (Malay); ulas-ulas.

Note — Most specimens are glabrous, but some younger ones still have a sericeous or hirsute indumentum. The more pilose specimens are not geographically restricted (4 specimens spread over Borneo, one in Sumatra), therefore this character is not considered to be of taxonomic importance.

**SYNDYOPHYLLUM**

**INTRODUCTION**

The genus *Syndyophyllum* is characterized by the opposite leaves with serrate margin; the interpetiolar, early caducous triangular stipules; the long, hardly branching inflorescences of which one originates per node and which have widely-spaced bundles of staminate flowers with one pistillate flower in between; the petals which are shorter than the sepals in staminate flowers and which are absent in pistillate flowers; the 3-locular ovary with one ovule per locule; the distinct style and hardly lobed stigmas; and the lobed, sericeous fruits.

The genus *Syndyophyllum* was established by Lauterbach and Schumann (Schumann & Lauterbach, 1901), in which they described *S. excelsum* based on material

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2) With assistance of Jaklien Gillis and Jos Huizer, students in Leiden.
collected by Lauterbach. Up to now this is the only flowering specimen known from New Guinea. Their dubiously described *S. trinervium* was shown by Pax (1914) to be a *Mallotus* species. Airy Shaw (1974) later recognized W Malesian specimens as a separate subspecies, *S. excelsum* subsp. *occidentale*. He discussed a possible species status for the W Malesian specimens, but because the flowering and fruiting material from New Guinea was very scarce and the main difference seemed to be the number of stamens (4 or 5 in New Guinea and 8–10 in Sumatra and Borneo), Airy Shaw did not regard the two taxa as distinct species. Besides the stamens there are some minor differences in hairiness and shape of the leaves; the New Guinea specimens can be very hirsute (i.e. the ones in Papua New Guinea) and the leaves are usually ovate instead of usually elliptic. In the present study a new difference is found, which is used to raise both subspecies to the rank of species. In New Guinea one petiole of each leaf pair bears an axillary bud and the position of the budding petiole alternates with each successive leaf pair. In W Malesia the axillary buds are always in the axils of the leaves, never on the petiole.

**Syndyophyllum** Lauterb. & K. Schum.


Tree, monoecious, branching sympodially. *Indumentum* consisting of simple hirsute or sericeous hairs, glabrescent. *Stipules* small, interpetiolar, triangular, base broad, caducous, especially outside sericeous. *Axillary buds* in the axils of leaves or on the petiole of one of the leaves. *Petiole* reniform in transverse section, not pulvinate, hirsute to sericeous. *Leaves* simple, distichous, opposite, symmetric; blade chartaceous, punctate; base slightly oblique, cuneate to broadly attenuate; margin slightly serrate, flat, with a gland on each tooth; apex rounded to acuminate, very apex usually mucronulate; upper surface pustular with white dots, latter forming food bodies in young leaves; lower surface smooth; venation pinnate, looped and joined near the margin, triplinerved, above and beneath slightly raised, tertiary (and quaternary) veins finely scalariform. *Inflorescences* axillary thyrses, one per axil, hardly branching, flattened, with dichasial groups of stamine flowers, often with one pistillate flower per cluster, mainly developing after the stamine flowers have dropped off. *Bracts* and *bracteoles* usually minute, triangular, mainly outside sericeous. *Pedicels* very short, only elongating in fruit. *Flowers* actinomorphic. *Sepals* 4 or 5, imbricate, basally united for at most 1/3, in stamine flowers membranous, in pistillate flowers basally thickened and margin membranous, often some with one or two glands along the margin, outside sericeous, inside (sub)glabrous. *Petals* shorter than sepals, absent in pistillate flowers and perhaps absent in *S. excelsum*, 2–4 in *S. occidentale*, ovate to obovate, apex rounded or irregular, membranous, glabrous. *Disc* lobes absent. *Stamens* 4 or 5 or 8–10, on a short torus, in two whorls, outer whorl epipetalous, free; filament filiform, glabrous; anther ± triangular, basifixied in a deep cleft, opening latro-introrse by a slit, glabrous; connective with an apical triangular appendage. *Pistil*: ovary
3-locular, densely hirsute; ovules one per locule, descending, epipalous, anatropous, attached in upper half of column; style 1, short, hirsute; stigmas 3, apically split into two lobes, above papillose, beneath hirsute; in staminate flowers a pistillode of at most 1 or 3 filiform 'stigmas'. Fruit a 3-lobed regma, subglobose, outside sericeous, glabrescent, inside glabrous, dehiscing septi- and loculicidally into 6 valves; wall thin, woody; septum with one splitting vein; column after dehiscence with a narrow, straight septum margin attached to it, apically broadened. Seeds 1–3 per fruit, brown, glossy, micropyle clearly visible; ariloid absent. Embryo seen when immature, no endosperm.

Distribution — Two species endemic in Malesia, one in N Sumatra and Borneo, the other in N New Guinea.

Notes — 1. The branching system in Syndyophyllum and Moultonianthus is very complex (see note 1 under Moultonianthus). In Syndyophyllum occidentale the axillary buds are in the axils of the leaves. In S. excelsum one of the axillary buds per leaf pair is formed on a petiole, the other petiole has the axillary bud at its base. The position of the ‘budding' petiole alternates per leaf pair.

2. The differences between the species may be greater. However, only one poorly flowering specimen of S. excelsum was examined, which seemed to lack petals and had fewer stamens.

KEY TO THE SPECIES OF SYNDYOPHYLLUM

1a. Axillary buds in axil of leaves. Leaves (ovate to) elliptic, subglabrous beneath. Sepals and petals present in staminate flowers. Stamens 8–10. — Sumatra, Borneo ................................................................. S. occidentale
b. One axillary bud per leaf pair halfway along a petiole. Leaves ovate (to elliptic), subglabrous to hirsute beneath. [Only sepals (or petals) present in staminate flowers. Stamens 4 or 5]. — New Guinea ............................... S. excelsum

Syndyophyllum excelsum Lauterb. & K. Schum. — Fig. 4b, Map 3


3) Based on one flowering specimen!
Tree up to 32 m high, d.b.h. up to 1.1 m, bole slightly fluted or with buttresses of c. 0.7 by 0.7 m; flowering branches 1.7–2 mm thick, smooth to pustular, hirsute in Papua New Guinea. Outer bark midbrown to red-brown to brownish black, smooth, irregularly flaking, 0.5–1 mm thick; inner bark red to reddish brown, brittle, 3–4 mm thick. Sapwood yellow-brown to orange to dark brown, 2–3 cm thick; heartwood orange-yellow to brown to red-black. Axillary bud of one leaf pair on petiole of leaf. Leaves: stipules 3.2–4.9 by 1–1.2 mm, margin entire, apex acute; petiole 4–9 mm long, hirsute especially in Papua New Guinea; blade ovate (to elliptic), 6–25 by 2.5–9.5 cm, index 2.2–3.8, apex rounded, mucronulate, above glabrous, glaucous when dry, beneath subglaucous to hirsute in Papua New Guinea, brown when dry, nerves 10–12 per side. Inflorescences up to 15.3 cm long, densely hirsute in Papua New Guinea. Floral bracts 1.5–2.1 by 0.6–1.1 mm, outside hirsute; bracteoles c. 0.8 by 0.3 mm, outside hirsute. Stamineate flowers c. 2 mm in diam.; pedicel more or less absent; sepals (or petals) 4, ovate, 0.8–1.2 by 0.3–0.6, subsericeous; petals probably absent; stamens 4 or 5, filament c. 2.2 mm long, anther c. 0.8 by 0.8 mm. Pistillate flowers not seen. Fruits c. 14 mm broad by 8 mm high; pedicel up to 7 mm long; wall c. 0.8 mm thick. Seeds ± globose, 7–8 mm in diam.; hilum c. 0.8 mm long. Embryo not seen.


Vernacular names — New Guinea, Irian Jaya: Besoembrij, kegboi, sekaijdjakka, siekoe, wobbryka (Manikiong); kelasawa, kloesaowe, kloesawa, koeloesawa (Mooi); ntoem (Kebar); makan (Kwerba); menom (Hattam). — Papua New Guinea: Dabi, falef, pispsis, sab (Amele); djakui, dumpahop, dzara, hawamp, malamamoi, sankei, sarenki, sisek, sumpiam (Dumpu); dumusi, mames, panama (Bilia); fai, golo, mont, sogi, wime (Faita).

Note — The specimens from Papua New Guinea are very hirsute on branches, leaves, and inflorescences, while the Irian Jaya specimens are more subglabrous like the W Malesian *S. occidentale*.

**Syndyophyllum occidentale** (Airy Shaw) Welzen, *stat. nov.* — Fig. 4a, c–h, Map 4


Tree up to 23 m high, girth up to 1.25 m, d.b.h. up to 40 cm (buttresses up to 70 cm); flowering branches 1.5–2 mm thick, smooth to pustular, sericeous when young. **Outer bark** (whitish to purplish) brown to very dark, smooth to lenticellate, scaling in large plates; **inner bark** dark orange brown to red, c. 6 mm thick, sticky.
Sapwood white; cambium yellowish to red. Axillary buds in axils of leaves. Leaves: stipules 3.2–4.9 by 1–1.2 mm, margin entire, apex acute; petiole 6–13 mm long, at most sericeous above in groove; blade (ovate to) elliptic, 8.2–31 by 2.3–12.5 cm, index 2.2–3.8, apex acute to acuminate, very apex rounded to mucronulate, above glabrous, dark green, beneath subsericeous, yellow-green, nerves 10–12 per side. Inflorescences up to 34 cm long, (sub)sericeous. Bracts to the cymes 1.7–4.4 by 0.7–1 mm, outside hirsute. Staminate flowers 2–3 mm in diam.; pedicel less than 0.5 mm long; sepals 5, ovate, 1.4–2 by 0.5–0.8 mm, subhirsute, especially the margin, whitish green; petals 2–4, 0.7–1.8 by 0.3–1.1 mm; stamens 8–10, filament 3.5–5.5 mm long, anther c. 1 by 0.7 mm; pistillode absent to 3 linear styles, up to 1.5 mm long. Pistillate flowers 2.0–2.5 mm in diam., pedicel 0.5–1.3 mm long; sepals 5, ovate, 1.2–2.1 by 0.6–1.2 mm, outside sericeous, inside glabrous; ovary ovoid, 1.3–2.1 by 1.3–2.8 mm broad, style 1–3.5 mm long, stigmas 5–8 mm long, upper 1–2 mm bifid. Fruits 14–19 mm broad by c. 8 mm high; pedicel up to 7 mm long, bright brown; wall c. 0.7 mm thick. Seed ± globose, 6.5–9 mm in diam., dark brown to black; hilum c. 0.8 mm long. Embryo only seen when immature, at least 6 by 5.3 mm, radicle c. 0.5 mm long.

Distribution — Malesia: N Sumatra and Borneo.

Habitat & Ecology — Found in primary forests along rivers. Soil: sandstone, black soil. Altitude 15–600 m. Fl. Mar.–Sep.; fr. May–Nov. Reported to be associated with ants (Argent et al. 108247); the ants are probably attracted by the food bodies produced by the young leaves on their upper surface. Presumably the small glands in the leaves (punctuation) secrete the food bodies.

Vernacular name — Borneo, Sabah: Bringguati (Dusun Banggi).

EXCLUDED TAXON


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IDENTIFICATION LIST

Material of Erismanthus, Moultonianthus, and Syndyophyllum studied:

1 = Erismanthus obliquus Wall. ex Müll.Arg.
2 = Erismanthus sinensis Oliv.
3 = Moultonianthus leembruggianus (Boerl. & Koord.) Steenis
4 = Syndyophyllum excelsum Lauterb. & K. Schum.
5 = Syndyophyllum occidentale (Airy Shaw) Welzen

A series 3549: 3; 16734: 3 — d’Alleizette 942: 2 — Argent & Saridan 9341: 1 — Argent et al. 108247: 5.
Endert 5004: 3.
Fraser 262: 5.
Hamid 10604: 1 — Henry 23: 2; 38: 2.
KEP FRI series 554: 1; 6594: 1 — Kerr 4046: 2; 6787: 2; 17642: 2; 18039: 2 — Kiah 24341: 1
— King's collector 8263: 1 — KL series 3380: 1 — Koorders 22285: 3 — Kostermans 5305: 5; 6700: 3; 21118: 1 — Kunstler 8263: 1.
Native collector 412: 3; 464: 3; 510: 3; 563: 3 — NGF series 46999: 4 — Nooteboom 1294: 5.
Omar 397: 3.
Paie 7735: 3 — Phengklai 1075: 2 — Phon 2034: 2 — Pierre 23 (Aug. 1868): 2; 23 (Sep. 1869): 2; 1310: 2; 5341: 1 — Poilane 1252: 2; 5217: 2; 6713: 2; 8316: 2; 9092: 2; 9372: 2; 9699: 2; 10212: 2; 13256: 2; 40792: 2 — Put 2652: 2.
Rahmat si Boeea 6302: 5 — Richards 2266: 3 — Ridley 2445: 1; 14693: 1.
S series 17019: 3; 20299: 3; 22847: 3; 23431: 3; 24563: 3; 41694: 3; 43396: 3 — SAN series 16098: 5; 16526: 3; 16836: 3; 16952: 3; 20866: 3; 32803: 3; 33336: 5; 35822: 5; 41669: 5; 53229: 5; 60248: 3; 63637: 3; 63801: 5; 64314: 5; 71520: 3; 76165: 5; 77583: 5; 77604: 5; 93863: 5; 95168: 3; 95269: 3; 97363: 5; 110022: 5; 111913: 5; 121252: 3; 124629: 3 — Sands 5708: 3 — Saunders 306: 4; 324: 4; 375: 4; 376: 4; 383: 4; 387: 4; 427: 4; 446: 4; 463: 4; 494: 4; 503: 4; 509: 4 — Sauveur 960: 5 — Schlechter 18378: 4 — Scortechini 1789: 1 — SF series 6263: 1 — Shah MS 1324: 1 — Smitinand 3172: 2; 10192: 2 — Soejarto, Smitinand, K. Taylor & Nantasan 6050: 2 — Soepadmo 845: 1 — Støersen, Larsen & Hansen 523: 2; 545: 2.
Vidal 4736: 2.
Wallich 8011: 1 — de Wilde & de Wilde-Duyfjes 14388: 5.