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REVISION OF THE GENUS PHAEANTHUS (ANNONACEAE)

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SUMMARY

A revision of the genus *Phaeanthus* Hook.f. & Thomson (Annonaceae) is presented. The genus comprises 8 species. A key to the fruiting and/or flowering specimens of the genus is included. The genus consists of shrubs to small-sized trees from Malesia and Vietnam. It is characterised by sepals and outer petals that are alike, numerous carpels and stamens, the latter truncate with a distinctive connective prolongation, monocarpous fruits, and leaves often drying dark brown to black. A phylogenetic analysis shows the monophyly of the genus and that *Phaeanthus nutans* can be considered the sister species of the remaining species.

Key words: Annonaceae, *Phaeanthus*, phylogeny, revision.

INTRODUCTION

The Annonaceae is a pantropical family with c. 130 genera and c. 2300 species. They occur primarily in tropical lowland rain forest, only a few species are confined to montane forest. The family has been subdivided formally and informally by different authors based on several character sets like flowers, fruits, pollen, etc. (Hutchinson, 1923, 1964; Sinclair, 1955; Fries, 1959; Walker, 1971; Van Setten & Koek-Noorman, 1992; Van Heusden, 1992; Keßler, 1993; Van Zuilen, 1996). Various opinions were proposed on the relationships of the genus. Based on a phenetic analysis of both flower and fruit characters Van Zuilen (1996) placed the genus *Phaeanthus* Hook.f. & Thomson in her informal group G together with the genera *Annickia*, *Enicosanthum*, *Ephedranthus*, *Malmea*, *Marsypopetalum*, *Neo-uvaria*, *Pseudephedranthus*, *Trivalvaria*, and *Woodiellantha*, of which several have been recently revised. This revision is considered as a precursor for the Flora Malesiana treatment.

VEGETATIVE MORPHOLOGY

The genus consists of shrubs to small-sized trees (exceptionally larger) with entire, alternate distichous leaves without stipules (Fig. 1a). The leaves are usually thin (papyraceous), the young leaves even membranous, except *Ph. impressinervius* Merr. which has pergamentaceous leaves. Furthermore, in comparison with many other Annonaceae genera, the leaves have a shiny appearance. The hairs are usually simple, but stellate hairs and scales have sometimes been observed. The indument may be long, dense

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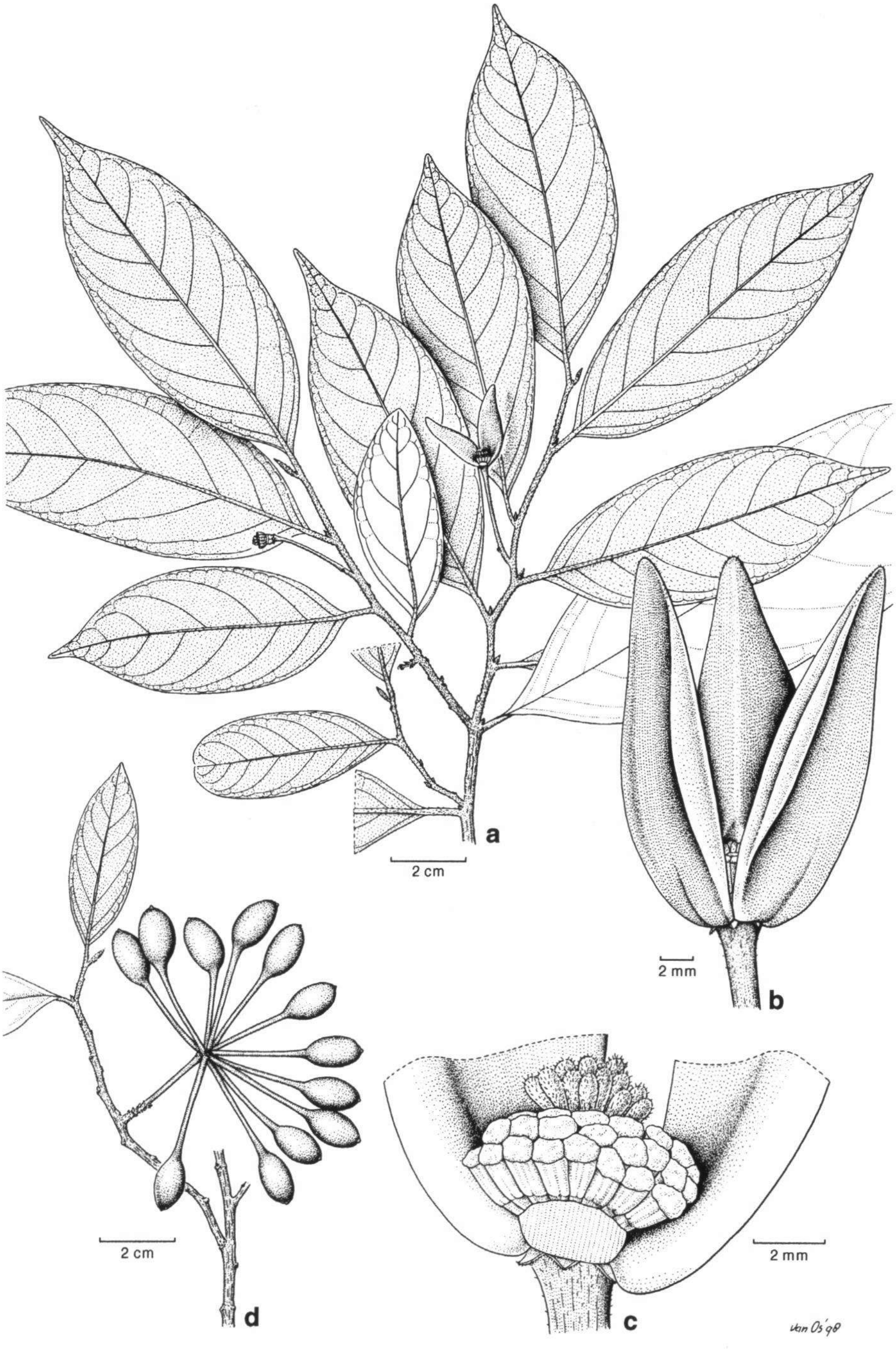


Fig. 1. *Phaeanthus ebracteolatus* (C. Presl) Merr. a. Habit; b. flower; c. flower with one inner petal removed; d. monocarps (a–d: *Ridsdale 1250*).

and soft. The leaves usually dry characteristically dark brown or even black. They sometimes have a shiny appearance on the upper side, which is very characteristic for *Ph. splendens* Miq. The venation pattern can be described as eucamptodromous with inconspicuous marginal loops (as described by Radford et al., 1974). Klucking (1986) shows leaf clearings of several species which in his terminology belong to the 'Late Phase Venation' or sometimes to the 'Minor Phase Venation' type.

INDUMENT

The indument of *Phaeanthus* consists of simple hairs. The following different types can be distinguished (terminology after Hewson, 1988): 1. Pilose (sometimes more dense, close to velvety); 2. strigose; 3. cobwebbed (hairs shorter than mentioned in the definition); 4. puberulous. The first two indument types are found all over the plant from branches to leaves to flowers. The term cobwebbed is used for the hairs on the stigmas only. The term puberulous is primarily used for hairs on the inner side of the inner petals.

Sometimes stellate hairs, scales and intermediates were found (Fig. 2a, b, intermediates not shown here). It has been concluded that these came from other plants and clung to the leaves of the *Phaeanthus* plants.

Most of these stellate hairs and scales are scattered over the leaf surface and rarely found in large quantities. All stellate hairs and scales appeared to be unattached, but were found, in small numbers, in nearly 90% of 400 specimens examined. When encountered in larger quantities the stellate hairs and scales appeared to be concentrated together. When compared to the scales and stellate hairs of other Annonaceae genera like *Neo-uvaria*, *Duguetia* (from South America) and *Rauwenhoffia* the stellate hairs and scales appeared to be quite similar. The main difference was the firm attachment of the scales and hairs of the latter.

Given the fact that the stellate hairs and scales are unattached and usually scarcely encountered on the leaves, the assumption arises that either the stellate hairs and scales are from other plants or thinly stalked and caducous. Stellate hairs and scales are never found on young leaves and branches, furthermore no remnants of stalks were found after scanning. Thus one may conclude that the hairs and scales may come from other plants and clung to the leaves of the *Phaeanthus* plants, even when the indument is strigose.

WOOD ANATOMY

The type specimen of *Ph. tephrocarpus* Merr. has vegetatively the appearance of a *Dichapetalum* spec. (Dichapetalaceae), the monocarps of all specimens were not attached to the twigs and the characteristic wood and bark appearance of the Annonaceae was not directly obvious. At first we doubted whether this specimen belonged to the Annonaceae.

Therefore a study of the wood and bark anatomy of branches of this specimen was undertaken in order to compare to the branchwood of other species of *Phaeanthus*. Unfortunately small diameter branches had to be used since mature stems were not

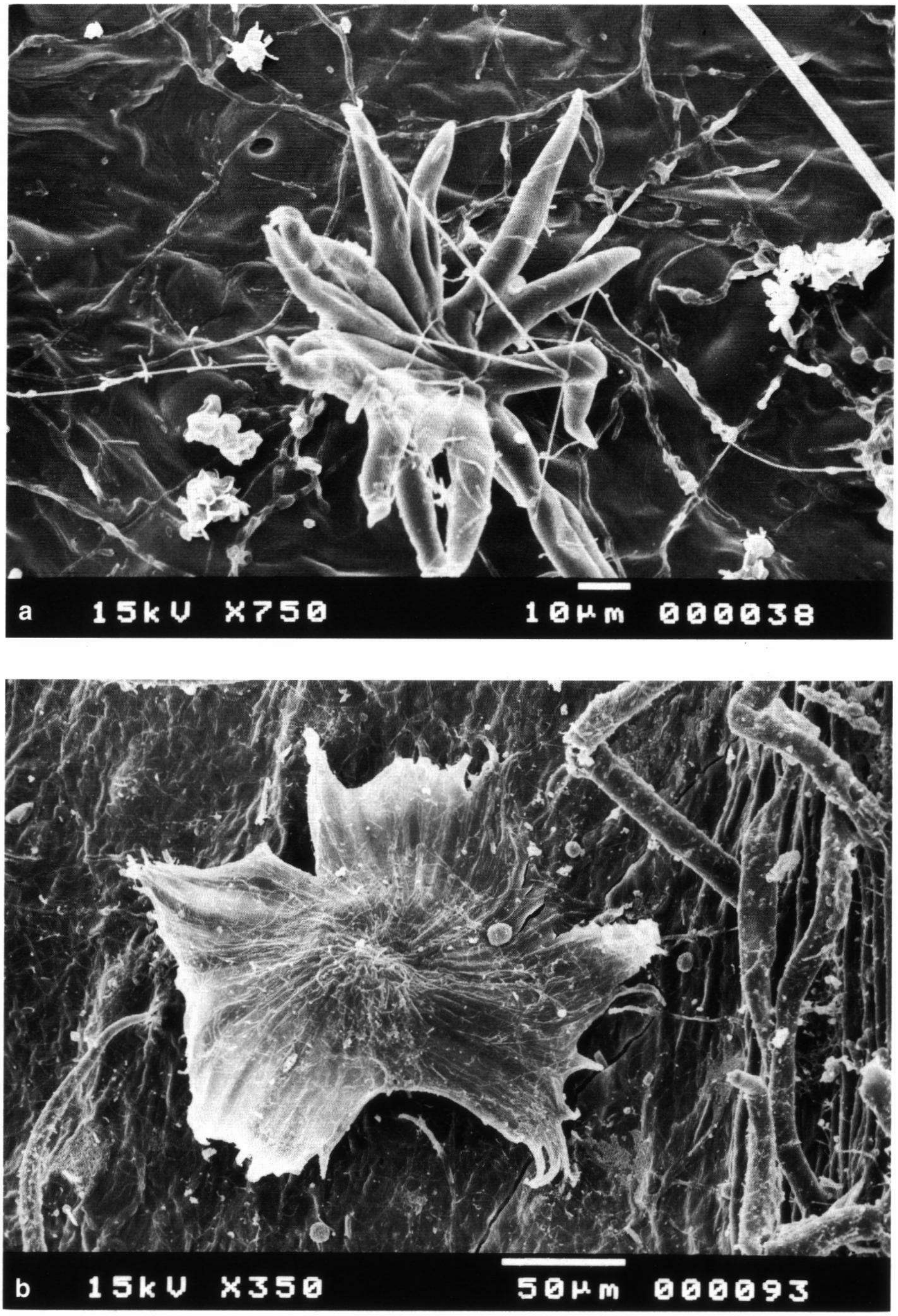


Fig. 2. a. Stellate hair found on *Phaeanthus nutans* Hook.f. & Thomson [*KEP/FRI 13403 (Loh)*; ×750]. – b. Scale found on *Ph. ebracteolatus* (C. Presl) Merr. [*Koorders 16024*; ×350].

available. Most other studies are based on the anatomy of stem wood and do not rely on the anatomy of younger branches, as the wood may show aberrant characteristics. The wood of the Annonaceae (Santos, 1929; Desch, 1955; Metcalfe & Chalk, 1950a; Metcalfe, 1987) is usually characterised by a combination of wide rays and narrow bands of axial parenchyma, which together produce a scalariform pattern in cross section. The phloem rays are usually dilated and have a triangular shape. Phloem fibres occur in bands alternating with sieve tubes, companion cells and phloem parenchyma.

Phaeanthus tephrocarpus appears to possess this combination of characters and is moreover a perfect match in stem anatomy with the other *Phaeanthus* species studied. It differs from Dichapetalaceae as the wood of the Dichapetalaceae usually is characterised by wide rays, and irregular and up to 8-cells-thick paratracheal parenchyma. Furthermore the phloem rays in the Dichapetalaceae are not dilated (Metcalfe & Chalk, 1950b).

Specimens studied:
Ph. ebracteolatus: *Coode 5428* (L), *Fallen, Lelean & Franklin 336a* (L); *Ph. nutans*: *KL 3526 (T. & P.)* (L); *Ph. splendens*: *Keßler PK 1561* (L); *Ph. sumatrana*: *De Wilde & De Wilde-Duyfjes 21286* (L); *Ph. tephrocarpus*: *Elmer 21860* (L), *SAN 91309 (Fedilis & Sumbing)* (L); *Ph. vietnamensis*: *Thai Thuan 124* (HN); *Ph. villosus*: *BS 30775 (Ramos & Edaño)* (L).

INFLORESCENCE AND FLOWERS

The flowers are arranged in 1–3, sometimes 4-flowered, densely bracteate inflorescences. The bracts are persistent. The inflorescence is a cyme which usually is reduced to one axis, except for *Ph. ebracteolatus* (C. Presl) Merr. where the cyme often is branched several times. The inflorescences are extra-axillary on the same side as the upper leaf of the internode, but sometimes appearing to be terminal. In fact the inflorescences only appear to be extra-axillary, originally they are either terminal or axillary, with a part of the inflorescence peduncle grown together with the branch. According to Fries (1919) the inflorescence of *Phaeanthus* originally is terminal. An axillary shoot then overtops the inflorescence and part of the peduncle grows together with the branch. In fruit the peduncle, pedicel and torus often increase in length and diameter. The flower buds are always conical-shaped with 3 valvate, free sepals. The outer petals are like the sepals. The sepals and the outer petals as well are usually persistent in fruit (otherwise scars are clearly visible). The inner petals are triangular with a broad base (Fig. 3). At the base there might be a glandular-like spot, characterised by an obvious colour difference from the rest of the petal tissue. The hemispherical torus (Fig. 4a) is covered with more or less dense hairs between the carpels, the part where the 40–100 truncate stamens are inserted appears to be glabrous. The stamens (Fig. 4b, c) have a distinct connective prolongation except for *Ph. splendens* and *Ph. impressinervius*. On top of the torus are 15–50 carpels (Fig. 4a), which are completely surrounded by the stamens. The carpels usually have only one ovule (rarely two), with true lateral placentation (Fig. 5e), except for *Ph. impressinervius* which has sublateral placentation (Fig. 5f) and *Ph. nutans* (Hook.f. & Thomson) which has a basilateral placentation (Fig. 5g).

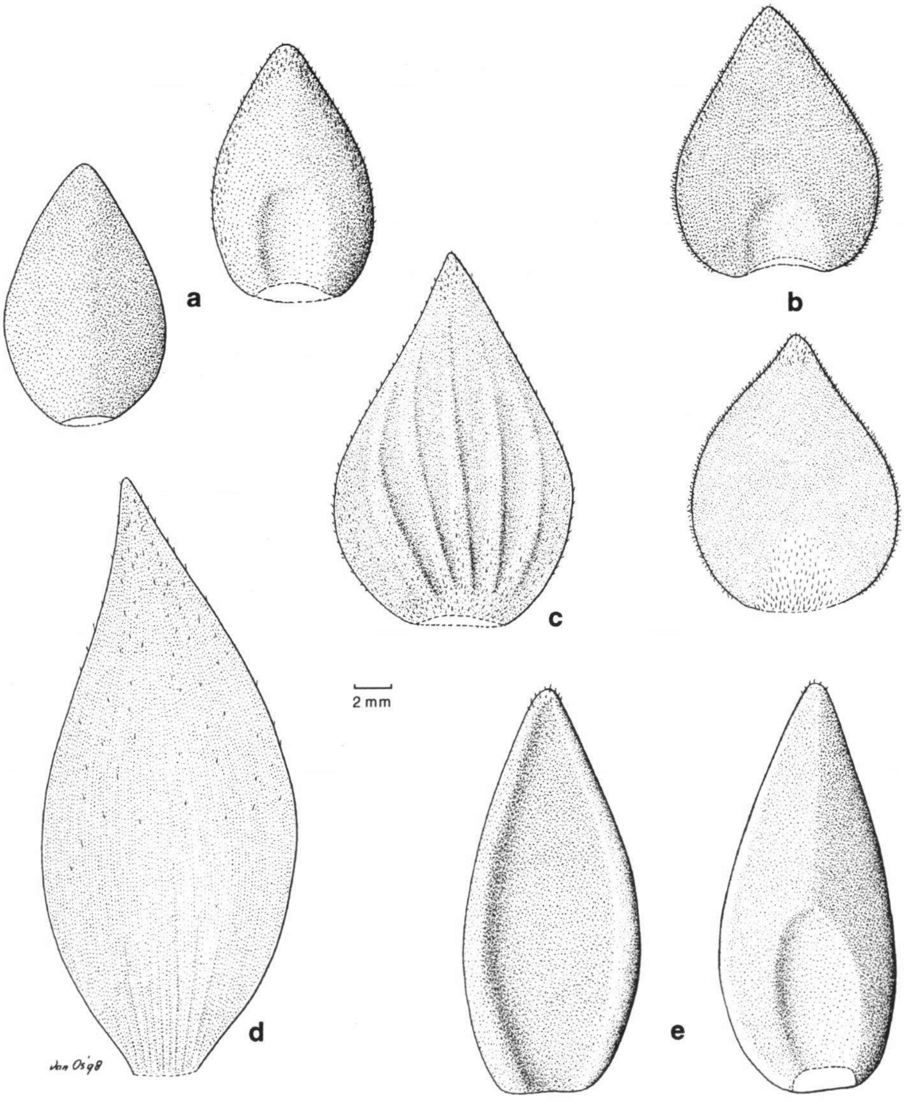


Fig. 3. Inner petals of mature flowers. a. *Phaeanthus splendens* Miq., interior (right), exterior (left); b. *Ph. sumatrana* Miq., interior (above), exterior (below); c. *Ph. nutans* Hook.f. & Thomson, exterior; d. *Ph. villosus* Merr., exterior; e. *Ph. ebracteolatus* (C. Presl) Merr., interior (right), exterior (left) [a: *Kostermans 4146*; b: *De Wilde & De Wilde-Duyfjes 18801*; c: *KEP/FRI 12307 (Whitmore)*; d: *BS 30775 (Ramos & Edaño)*; e: *Ridsdale 1250*].

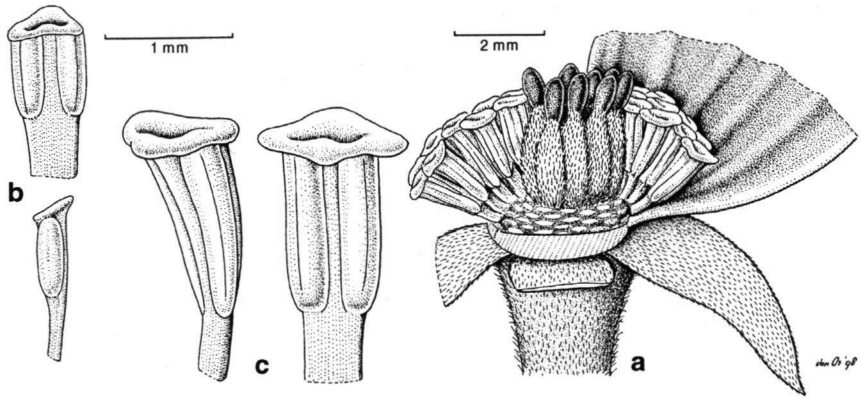


Fig. 4. a. Carpel/stamen arrangement of *Phaeanthus nutans* Hook.f. & Thomson, flower with removed outer petals and stamens. – b & c. Stamens. b. *Ph. splendens* Miq., with connective prolongation not covering thecae, lateral (below) and abaxial (above); c. *Ph. nutans* Hook.f. & Thomson, with connective prolongation covering thecae, lateral (left) and abaxial (right) [a, c: *KEP/FRI 12307 (Whitmore)*; b: *Kostermans 4146*].

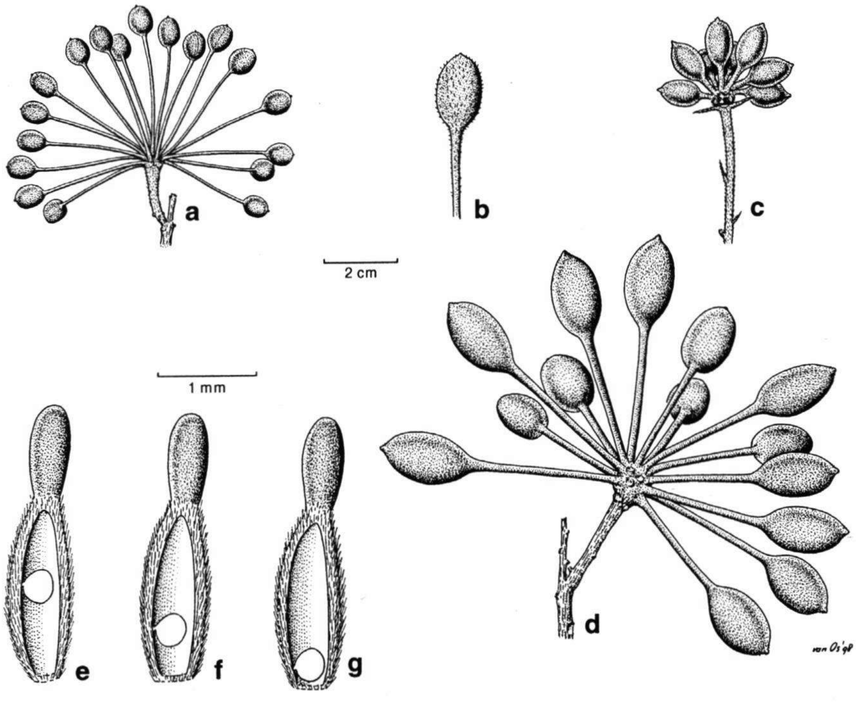


Fig. 5. a–d. Monocarps. a. *Phaeanthus ebracteolatus* (C. Presl) Merr.; b. *Ph. tephrocarpus* Merr.; c. *Ph. nutans* Hook.f. & Thomson; d. *Ph. splendens* Miq. – e–g. Carpel with ovule placentation (schematic). e. lateral placentation; f. sublateral placentation; g. basilateral placentation [a: *Elmer 17183*; b: *Elmer 21860*; c: *KEP/FRI 12307 (Whitmore)*; d: *Kostermans 4146*].

CARPIDIA

The shape of the monocarps (Fig. 1d, 5a–d) of the different species does not vary much. They usually are ellipsoid except in *Ph. ebracteolatus* (Fig. 1d, 5a), where they may be globose. But the monocarps do vary considerably in size. The monocarps are almost always glabrous except in *Ph. tephrocarpus*. The lengths of the pedicel and peduncle do not differ much from the ones in the inflorescence, they may only become thicker when in fruit. The monocarp wall is usually thin (0.25–0.5 mm), only in *Ph. splendens* and *Ph. tephrocarpus* can it reach one millimetre in thickness. Each monocarp has one seed, rarely two. When they have two seeds, the monocarp does not become moniliform, but the second seed is obtusely placed on top of the basal seed. The seed is always ellipsoid in shape, having a ruminate endosperm and a pale brown to ochre colour. The raphe is a shallow to distinct groove, usually straight but sometimes slightly bent. The hilum is transversely elliptic to somewhat circular. The seed wall is very thin. The ruminations are lamellate in four parts, which can clearly be seen when the seed is transversely cut (as shown by Van Setten & Koek-Noorman, 1992). The hypodermis contains cubic cells with crystals and the mesotesta is made up of transverse fibres. The outer integument is prolific in the seed. No middle integument is distinguishable and the inner integument is pressed into one small layer. Furthermore no oil idioblasts are found and the nucellus is resorbed (as stated by Christmann, 1987).

PHYLOGENY

A phylogenetic analysis was performed to establish the relationships between the different species of the genus. Two species of two other genera were used as outgroups:

1. *Trivalvaria macrophylla* (Blume) Miq. In several of the previously mentioned 'classical' classifications *Trivalvaria* Miq. is placed in the same divisions as *Phaeanthus*, also Van Zuilen (1996) places *Trivalvaria* very close to *Phaeanthus* using a cluster-analysis.
2. *Popowia pisocarpa* (Blume) Endl. According to a preliminary study by Bygrave (in prep.) based on cpDNA, *Popowia* Endl. cannot be distinguished from *Phaeanthus*.

Additionally a species of the genus *Miliusa* Lesch. ex A.DC. has been used as an outgroup, but the characters of *Miliusa* used in this analysis were not different enough to clearly separate this species from the ingroup. All the character states for the outgroups were scored from herbarium material housed at L. The analysis was based on the following 16 characters (for data matrix see Table 1):

1. Leaf surface (primarily on upper side)
   0 = dull; rough
   1 = shiny
   2 = very shiny

2. Pairs of secondary veins
   0 = 9–15
   1 = 16–20

3. Inflorescence type
   0 = cyme
   1 = cyme reduced to one axis
   2 = fascicle

4. Position of inflorescence or single flower
   0 = axillary
   1 = leaf-opposed
   2 = extra-axillary

5. Bract length
   0 = < 4 mm
   1 = ≥ 4 mm

6. Shape of outer petals
   0 = obovate
   1 = triangular

7. Fusion of sepals and petals
   0 = free
   1 = connate

8. Shape of outer petals
   0 = resembling inner petals
   1 = resembling sepals

9. Number of stamens
   0 = ≥ 110
   1 = 80–100
   2 = 20–80
   3 = ≤ 20

10. Connective prolongation
    0 = covering thecae
    1 = not covering thecae

11. Number of carpels
    0 = ≥ 60
    1 = 30–60
    2 = ≤ 30

12. Placentation
    0 = lateral
    1 = sublateral
    2 = basilateral
    3 = basal

13. Monocarp-stipe length
    0 = ≤ 1.25 cm
    1 = > 1.25 cm

14. Monocarp shape
    0 = long ellipsoid
    1 = ellipsoid
    2 = globose

15. Monocarp size (length × width)
    0 = ≤ 1 cm^2
    1 = 1–2 cm^2
    2 = ≥ 2 cm^2

16. Monocarp-wall thickness
    0 = < 0.75 mm
    1 = ≥ 0.75 mm

The data matrix was analysed in PAUP version 3.1.1 (Swofford, 1993), with the characters treated as unordered. Options used were: mulpars, branch and bound option, minimal trees only, addition sequence furthest. Bootstrap values (Felsenstein, 1985; 1000 replicates, settings as before) of more than 50% are indicated in the figure. The decay indices were obtained by comparing the resolved branches in strict consensus cladograms of up to 5 steps longer with the most parsimonious cladogram.

Table 1. Data matrix for the phylogenetic analysis of the genus *Phaeanthus* with *Trivalvaria macrophylla* (Blume) Miq. and *Popowia pisocarpa* (Blume) Endl. as outgroups. In case of polymorphism **bold** indicates the primitive character state, this was deduced after the analysis. For characters and character states see text.

Taxa \ Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
T. macrophylla	0	0	2	2	0	1	0	0	1	0	1&2	3	0	0	1	0
P. pisocarpa	0	0	2	1	0	1	1	0	3	0	2	2	0	2	0	0
Ph. nutans	1	0	1	2	1	0	0	1	1	0	2	2	0	1	0&1	0
Ph. splendens	2	0	1	2	0	0	0	1	2	1	1	0	1	1	2	1
Ph. sumatrana	1	1	1	2	0&1	0	0	1	1	0	1&2	0	1	1	1	0
Ph. ebracteolatus	1	0	0	2	0	0	0	1	2	0	1	0	0&1	1&2	0&1	0
Ph. villosus	1	1	1	2	0	0	0	1	1	0	1	0	?	?	?	?
Ph. tephrocarpus	1	0	1	2	?	0	?	?	?	?	?	?	1	1	2	1
Ph. vietnamensis	1	0	1	2	0&1	0	0	1	1	0	2	0	1	1	1	0
Ph. impressinervius	1	0	1	2	0	0	0	1	2	1	2	1	?	?	?	?

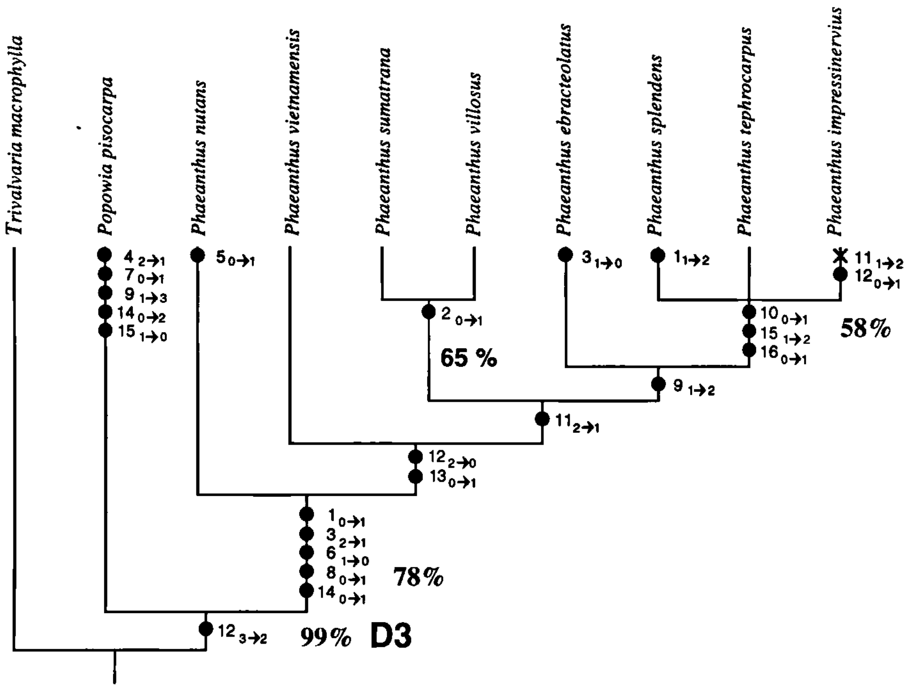


Fig. 6. Strict consensus cladogram of the three most parsimonious cladograms after analysis of dataset (see Table 1). Cladogram is 32 steps long; ci = 0.97; ri = 0.93. The character state changes have been indicated. Bootstrap values of 50% and higher are stated at the nodes. D = decay index.

Three most parsimonious cladograms were found, of which the strict consensus cladogram is shown in Fig. 6. The cladogram is 32 steps long (including 8 steps for polymorphic taxa) with a consistency index of 0.97 and a retention index of 0.93.

It is empirically demonstrated (Hillis & Bull, 1993) that bootstrap values of 70% and higher correspond to a probability level of 95%. Thus bootstrap values of 70% and higher indicate statistically significant groups. In the strict consensus cladogram the bootstrap value (78%) significantly supports *Phaeanthus* as a genus. The decay index of the genus proved to be 3, which indicates that the genus first branches off with a cladogram of three steps longer than the strict consensus cladogram. Within the cladogram two other branches are supported by high bootstrap values (of 65% and 58%), but these are not significant.

The first branch shows *Ph. nutans* as the sister species of the rest of the genus, followed by *Ph. vietnamensis*. The third branch shows *Ph. sumatrana* and *Ph. villosus* as sister species. Subsequently, *Ph. ebracteolatus* branches off. The cladogram ends with *Ph. splendens, Ph. tephrocarpus,* and *Ph. impressinervius* as a trichotomy (which is fully resolved in the most parsimonious cladograms). Flowering material of *Ph. tephrocarpus* and fruiting material of *Ph. villosus* and *Ph. impressinervius* are needed to resolve the relationship in the trichotomy. The same accounts for the relationship between *Ph. villosus* and *Ph. sumatrana.*

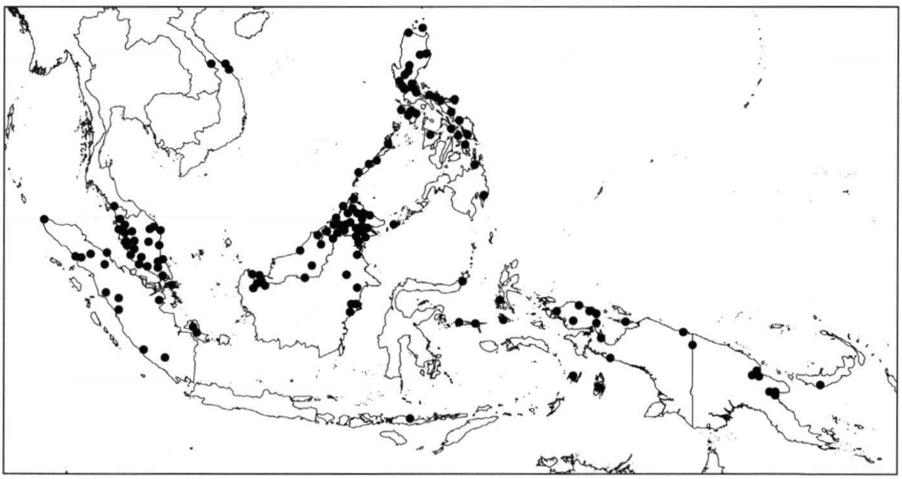
The cladogram contains one reversal for *Ph. impressinervius* where the number of stamens decreases.

KEYS AND DESCRIPTIONS

PHAEANTHUS — Map 1

Phaeanthus Hook.f. & Thomson, Fl. Ind. 1 (1855) 146; Miq., Fl. Ned. Ind. 1, 2 (1858) 51; Boerlage, Handl. Fl. Ned. Ind. 1, 1 (1890) 25; J. Sinclair, Gard. Bull. Straits Settlem. 14 (1955) 373; Fries in Engl. & Prantl (ed.), Nat. Pflanzenfam., ed. 2, 17 A, 2 (1959) 140; Johns, The flowering plants of Papuasia, 1. Magnoliidae (1987) 34; Keßler in Kubitzki et al. (ed.), The families and genera of vascular plants 2 (1993) 121. — Type species: *Phaeanthus nutans* Hook.f. & Thomson.

Shrubs or trees up to 25 m tall. *Old branches* terete, brown to ash-grey when dried, bark with lozenge-shaped striations; young branches terete or slightly flattened, black or reddish brown when dried; covered with lenticels and (sometimes) transverse scars. *Petioles* black, longitudinal (slightly) grooved or flattened (*Ph. tephrocarpus*). *Leaves* (narrowly) obovate to elliptic, papyraceous to pergamentaceous (*Ph. impressinervius*), often membranous when young, shiny appearance, often turning black when dried; base obtuse to cuneate (seldom rounded); apex acuminate (to cuspidate); midrib sunken above, prominent below, secondary veins straight, anastomosing; reticulation hardly (or not) visible above. *Inflorescences* extra-axillary or sometimes terminal, cymose, short peduncled, 1–4-flowered; peduncle brown or black when dried; pedicel brown or reddish brown when dried. *Flowers* bisexual. *Bract(s)* 1 (or 2), triangular, sessile, apex acute, persistent; bracteole (0 or) 1, bract-like. *Sepals* 3, valvate, triangular, apex acute. *Outer petals* 3, valvate, sepal-like, much smaller than inner ones; sepals and outer petals usually persistent in fruit. *Inner petals* 3, valvate, triangular, base broad, apex acute to rounded, glandular-like structure at base. *Torus* hemispherical. *Stamens* 30–100, truncate (wedge-shaped), filament short, connective prolongation flat, oblique, edges wavy, prolongation usually covering the thecae; anthers 2, extrorse with visible connective. *Carpels* 15–60, cylindrical, appressed rusty or ochre strigose; style short or absent; stigma ellipsoid to club-shaped; ovule(s) 1 (or 2), lateral to basilateral (*Ph. nutans*). *Monocarps* many (up to 60), ellipsoid (to globose), black when dry,



Map 1. Distribution of the genus *Phaeanthus* Hook.f. & Thomson.

apiculate, raphe visible when dry; stipe rounded (to angular), sometimes grooved and black when dried. *Seed(s)* 1 (or 2), ellipsoid, seed coat papyraceous, ruminations lamellate in 4 parts.

Distribution — Vietnam, Malesia: Malaysia, Singapore, Indonesia (except Java), Brunei, Philippines, Papua New Guinea.

Notes — A chromosome count of somatic meristematic cells of a root tip of a seedling of *Ph. ebracteolatus* (Okada, 1987, sub *Ph. macropodus*) revealed 2n = 18 chromosomes. The same was revealed on a count of a specimen from Sumatra (material not seen; Okada & Ueda, 1984). Walker (1971) studied the pollen of *Ph. splendens* and *Ph. ebracteolatus*: the grains were solitary, apolar and radiosymmetric, the exine surface is more or less smooth to weakly verrucate. At least one species, *Ph. ebracteolatus*, is known to contain an alkaloid called phaeanthine in its bark and leaves (Aguinaldo et al., 1985). It is considered to be the active ingredient of a widely used remedy for sore eyes in the Philippines (Perry & Metzger, 1980). *Phaeanthus ebracteolatus* is the only species tested for the alkaloid, but *Ph. splendens* [*S 47399 (Awa & Paie), S 55655 (Hock)*] and *Ph. sumatrana* [*Diepenhorst HB 3100* (U)] are also said to be used as a remedy against the same illness.

KEY TO THE SPECIES

1a. Leaves with (13–)15–20 pairs of secondary veins 2
b. Leaves with 9–15 pairs of secondary veins 3
2a. Pedicels 2.3–5 cm long; petals 1.3–2.2(–3.3) cm long, with short hairs inside; sepals pilose or glabrous inside; carpels 25–35; monocarps 1.3–1.8 cm long. — Sumatra, Peninsular Malaysia .... **5. Ph. sumatrana**
b. Pedicels 6.5–7.7 cm long; petals 2.5–3.7 cm long, glabrous inside; sepals glabrous inside; carpels 40–50; monocarps not seen. — Philippines .... **8. Ph. villosus**
3a. Leaves very shiny (primarily above) or silvery; monocarps 1.8–3 cm long .. 4
b. Leaves shiny; monocarps 0.8–1.8 cm long 5
4a. Leaves very shiny above; petals coriaceous; monocarps (2–)6–15, 1.9–3 cm long, glabrous; connective prolongation not covering thecae. — Sumatra, Peninsular Malaysia, Borneo .... **4. Ph. splendens**
b. Leaves shiny silvery grey; monocarps 35–60, 1.8–2.2 cm long, hairy. — Borneo .... **6. Ph. tephrocarpus**
5a. Sepals 3–9 mm long, hairy inside; petals with 5–7 prominent veins; placentation basilateral. — Peninsular Malaysia .... **3. Ph. nutans**
b. Sepals 1–4 mm long, glabrous inside; petals without prominent veins; placentation (sub)lateral 6
6a. Leaves pergamentaceous; connective prolongations not covering thecae; placentation sublateral. — Borneo .... **2. Ph. impressinervius**
b. Leaves papyraceous; connective prolongations covering thecae; placentation lateral 7
7a. Lowest bracts 3–4 mm long, other bracts 1–2.5 mm long; carpels 10–20. — Vietnam .... **7. Ph. vietnamensis**
b. Lowest bracts like other bracts, 1–2.25 mm long; carpels 30–50. — Lesser Sunda Islands, Borneo, Philippines, New Guinea .... **1. Ph. ebracteolatus**

SYNOPTICAL KEY TO THE SPECIES

The numbers refer to the same species as in the key above and the species descriptions. Numbers cited under more than one lead of a couplet are indicated in **bold**. When a given character is unknown for a species this number is omitted.

Tree height
- a) < 7 m
  __1__-2-__3__-__4__-5-__7__-8
- b) 7–15 m
  __1__-__3__-__4__-6-__7__
- c) > 15 m
  __1__-__4__

Leaf appearance
- a) shiny
  1-2-3-5-7-8
- b) very shiny (primarily on the upper side)
  4
- c) shiny silvery
  6

Leaf texture
- a) papyraceous (often membranous when young)
  1-3-4-5-6-7-8
- b) pergamentaceous
  2

Number of secondary vein pairs
- a) < 15
  1-2-__3__-4-__5__-6-7
- b) > 16
  __3__-__5__-8

Pedicel length
- a) < 1 cm
  __1__-__7__
- b) 1–5.4 cm
  __1__-2-__3__-4-__5__-6-__7__
- c) > 6.5 cm
  __3__-__5__-8

Bract length
- a) < 2.5 mm
  __1__-2-__3__-4-__5__-__7__-__8__
- b) 2.5–5 mm
  __1__-__3__-__5__-__7__-__8__
- c) > 5 mm
  __3__

Lowest and higher bracts
- a) of the same size
  1-2-3-4-5-8
- b) lowest bract larger than higher bracts
  7

Number of flowers per inflorescence
- a) 1
  __1__-2-__3__-__4__-__5__-7-__8__
- b) 2
  __1__-__3__-__4__-__5__-__8__
- c) 3
  __1__-__4__
- d) 4
  __1__

Sepal and inner petals length
- a) < 2 mm
  1-2-4-__5__-7-8
- c) 2–4
  __3__-__5__-6
- d) > 4 mm
  __3__

Sepal indument inside
- a) absent
  1-2-4-7-8
- b) present
  3-5-6

Petal length
- a) < 1 cm
  __4__-__7__
- b) 1–2 cm
  __1__-2-__3__-__4__-__5__-__7__
- c) 2–3 cm
  __1__-__3__-__4__-__5__-__8__
- d) > 3 cm
  __1__-__5__-__8__

Petal texture
- a) < 1 mm
  __1__-2-5-7-8
- b) 1–1.5 mm
  __1__-3
- c) > 1.5 mm
  4

Petal indument inside
- a) absent
  1-8
- b) present
  2-3-4-5-7

Petal veins
- a) not visible (without boiling)
  1-2-4-5-7-8
- b) prominent
  3

Number of stamens
- a) < 60
  1
- b) 60–95
  1-2-3-4-5-7-8
- c) > 95
  3-5

Stamen length
- a) < 1 mm
  7
- b) 1–2 mm
  1-2-3-4-5-7-8
- c) 2–2.5 mm
  1-3-5-8
- d) > 2.5 mm
  1-8

Number of carpels
- a) < 20
  3-7
- b) 20–40
  1-2-4-5
- c) > 40
  1-4-8

Carpel length
- a) < 2 mm
  1-2-3-4-5-7-8
- b) > 2 mm
  1-5-8

Connective prolongation
- a) covering thecae
  1-3-5-7-8
- b) not covering thecae
  2-4

Placentation
- a) lateral
  1-4-5-7-8
- b) sublateral
  2
- c) basilateral
  3

Stipe length
- a) < 1 cm
  1-3

Stipe length (*continued*)
- b) 1–2.6 cm
  1-3-4-5-6-7
- c) > 2.6 cm
  1-4

Monocarp number
- a) ≤ 15
  1-3-4-5-7
- b) 16–35
  1-5-7
- c) ≥ 36
  6

Monocarp length
- a) < 1 cm
  1
- b) 1–2.2 cm
  1-3-4-5-6-7
- c) > 2.2 cm
  4

Monocarp indument
- a) glabrous
  1-3-4-5-7
- b) strigose
  6

Monocarp wall thickness
- a) < 0.5 mm
  1-3-4-5-6-7
- b) 0.5–0.75 mm
  1-4-6
- c) > 0.75 mm
  4-6

Distribution
- a) Vietnam
  7
- b) Peninsular Malaysia, Sumatra
  3-4-5
- c) Borneo
  1-2-4-6
- d) Philippines
  1-8
- e) Lesser Sunda Islands, Sulawesi, Moluccas, Kai Islands, Aru Islands, New Guinea
  1

1. Phaeanthus ebracteolatus (C. Presl) Merr. — Fig. 1; Map 2

Phaeanthus ebracteolatus (C. Presl) Merr., Philipp. J. Sci., Bot. 3 (1908) 225; Sp. Blancoan. (1918) 128; Enum. Philipp. Fl. Pl. 2 (1923) 165. — *Uvaria ebracteolatus* C. Presl, Reliq. Haenk. 2 (1835) 77. — Type: *Haenke s.n.* [holo PR (acc. number 212924 B); iso PR], Philippines, Portus Sorzogon in insula Luzon, fr.

Uvaria tripetala Blanco non Roxb., non Lam., Fl. Filip. (1837) 465. — *Unona tripetala* 'sphalm.' (Blanco) Blanco non DC., Fl. Filip. ed. 2 (1845) 324. — Type: *Merrill Species Blancoanae 305* (holoneo PNH†, designated by Merrill, 1918; isoneo A, BM, K, L, P, US), Philippines, Luzon, Camarines Prov., fr.

Phaeanthus cumingii Miq., Fl. Ned. Ind. 1, 2 (1858) 51. — Type: *Cuming 525* (hololecto L, designated here; isolecto BM, K, P, SING, W), Philippines, fl.

Monoon macropodum Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1865) 17, syn. nov. — *Guatteria macropoda* Zipp. ex Burck, Nova Guinea 13 (1911) 429. — *Phaeanthus macropodus* (Miq.) Diels, Bot. Jahrb. Syst. 49 (1912) 161. — Type: *Zippelius 191* (holo L, barcode 0046168; iso A, L, barcode 0046183), Indonesia, Irian Jaya, fr.

Phaeanthus crassipetalus var. *papuana* Scheff., Ann. Jard. Bot. Buitenzorg 2 (1885) 29, syn. nov. — Type: *Teijsmann 17824* (hololecto BO, designated here), Indonesia, Halmaheira, Galela, fr.

Phaeanthus schefferi Boerl. ex Koord., Meded. Lands Plantentuin 19 (1898) 337; Valeton, Icon. Bogor. 2 (1907) 65, pl. 226, syn. nov. — Type: *Koorders 16024* (hololecto BO, designated here; isolecto L), Indonesia, Sulawesi, Minahasa, Ratahan, fr.

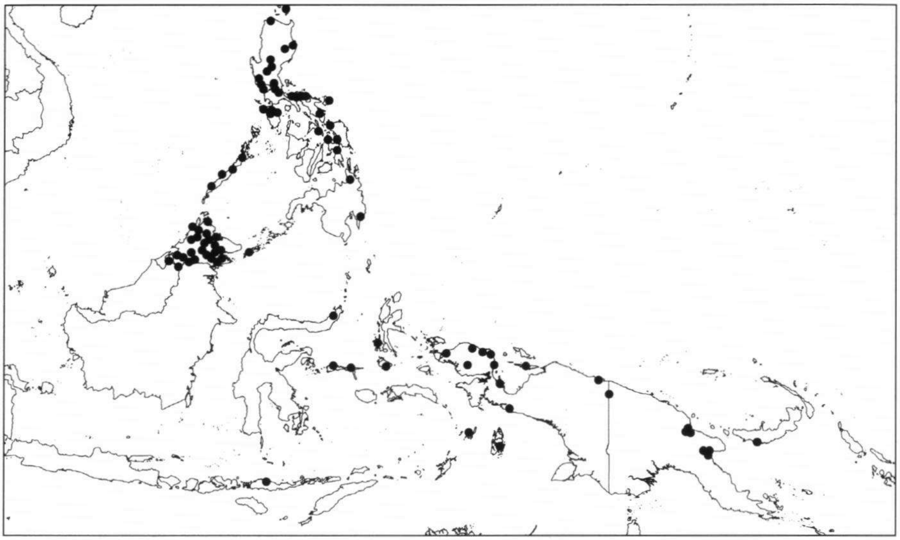
Phaeanthus macropodus var. *mollifolius* Diels, Bot. Jahrb. Syst. 49 (1912) 162, syn. nov. — Type: *Atasrip 65* (hololecto BO, n.v., designated here; isolecto L), Indonesia, Irian Jaya, fr.

Phaeanthus nigrescens Elmer, Leafl. Philipp. Bot. 5 (1913) 1728; Merr., Enum. Philipp. Fl. Pl. 2 (1923) 165, syn. nov. — Type: *Elmer 13727* (holo PNH†; iso A, K, L, U), Philippines, Mindanao, Agusan Prov., Cabadbaran, Mt Urdaneta, fr.

Phaeanthus nitidus Merr., Philipp. J. Sci., Bot. 11 (1916) 8, syn. nov. — Type: *BS 23477 (Ramos)* (holo PNH†; iso A, K, P), Philippines, Luzon, Sorsogon Prov., fr.

Phaeanthus pubescens Merr., Philipp. J. Sci. 14 (1919) 390; Enum. Philipp. Fl. Pl. 2 (1923) 165, syn. nov. — Type: *BS 27333 (Ramos)* (holo PNH†; iso A, K, P), Philippines, Luzon, Ilocos Norte Prov., Burgos, fr.

Shrubs or trees, 1–20 m tall, 1–35 cm diam. *Outer bark* dark grey or brown-grey, glabrous; inner bark cream or ochre; wood yellow to white. *Old branches* glabrous to pilose to strigose; young branches 1–4 mm diam., pilose to strigose; internodes 0.4–3.1 cm long. *Vegetative buds* pilose to strigose. *Petioles* 3–7(–11) mm long, 1–3 mm diam., pilose to strigose, glabrescent. *Leaves* 7.4–25.3 by 2.6–10.1 cm; glabrous or midrib short to long pilose or strigose above, midrib and lateral veins (sparsely) pilose to strigose below; veins 9–14 pairs, at an angle of 25–55° to the midrib, anastomosing 1–3(–6) mm from the margin. *Cymes* sometimes reduced to one axis, 1–4-flowered; peduncles 1–9(–13) mm long, 1–2 mm diam., pilose to strigose, glabrescent; pedicels (0.5–)1.2–3.0(–4.1) cm long, 1–1.5 mm diam., (sparsely) pilose to strigose. *Bract(s)* 1 (or 2), 0.75–2.25(–3.5) by 0.75–1.5 mm, appressed pilose to strigose outside, glabrous inside; bracteole 1, 0.5–2 by 0.5–1.5 mm, placed up to halfway the pedicel. *Sepals* 0.5–1.75 by 0.75–1.75 mm, 0.1–0.2 mm thick, appressed pilose to strigose outside, glabrous inside. *Inner petals* 1.2–2.9(–3.9) by 0.5–1.2(–2) cm, 0.5–0.75(–1) mm thick, margins, base and apex pilose to strigose outside, 4–6 veins visible when boiled, glabrous inside. *Torus* 1.5–4 mm wide, 1–3 mm high, pilose to strigose. *Stamens* 30–85, 1.25–2.25(–3) mm long, 0.75–1 mm wide at the apex, 0.25–0.66 mm wide at the base; thecae 1–2 by 0.2 mm. *Carpels* 20–50, 1.25–2.5(–3) by 0.5–1 mm; stigma sessile, 0.5–1.25 by 0.25–0.5 mm, margins and top cobwebbed, glabrescent; ovule(s) 1 (or 2), lateral. *Monocarps* (3–)15–35, 0.8–1.7(–2.1) cm long, 5–10(–15) mm diam., sometimes more globose than ellipsoid, apex 0.5–2 mm long, base and apex sparsely strigose; stipe (0.6–)1.3–3.1 cm long, 0.75–2 mm diam., pilose to strigose. *Seed(s)* 1 (or 2), 0.6–1.6 cm by 4–10 mm; monocarp wall 0.33–0.5(–0.75) mm thick.



Map 2. Distribution of *Phaeanthus ebracteolatus* (C. Presl) Merr.

Distribution — Malesia: Brunei, Sabah, Kalimantan Timur, Philippines, Sulawesi, Lesser Sunda Islands, Moluccas, Kai Islands, Aru Islands, Irian Jaya, Papua New Guinea.

Habitat & Ecology — Understorey tree in primary or secondary lowland forests; on steep hills especially on ridges, on riversides and on open places; on calcareous, rocky, clay, alluvial, loamy, or limestone soils. Altitude up to 800 m. Flowering: throughout the year. Fruiting: throughout the year.

Field notes — Leaves shiny dark green above, pale green below; veins yellowish. Flowers yellow to cream when mature. Monocarps green to yellow to orange when young, dark red to purple when mature. Indument colour ochre or rusty or chestnut-brown.

Note — The flowering specimens from Borneo belong with no doubt to this species. The fruiting specimens all have short stipes and monocarps of c. 1 cm, thus resemble *Ph. nutans* except that the bracts, sepals and outer petals are smaller compared to those of *Ph. nutans*. When comparing the leaves of the fruiting and flowering specimens we came to the conclusion that these belong to the same species. Unfortunately no collection has both flowers and monocarps at the same time. Sometimes larger fruits have been recorded, often being a result of gall infections.

2. Phaeanthus impressinervius Merr. — Map 3

Phaeanthus impressinervius Merr., J. Straits Br. Roy. Asiat. Soc. 85 (1922) 186. — Type: *BS 1792 (Ramos)* (holo PNH†; iso A, K, P), Malaysia, Sabah, Sandakan and vicinity, fl.

Shrubs. *Old branches* glabrous to sparsely strigose (to short pilose); young branches 1–3 mm diam., sparsely strigose (to short pilose); internodes 1–2.1 cm long. *Vegetative buds* strigose. *Petioles* 6–13 mm long, 1.5–2 mm diam., pilose to strigose, glabrescent. *Leaves* 11.5–20.9 by 3.7–7.9 cm, pergamentaceous; apex sometimes acute; glabrous above, midrib short to long pilose, midrib and lateral veins sparsely strigose below; veins 11–15 pairs, at an angle of 30–45° to the midrib, anastomosing 2–6 mm from the margin. *Cymes* reduced to one axis, 1-flowered; peduncles 4 mm long, 1 mm diam., strigose, glabrescent; pedicels 1.3 cm long, 1–1.5 mm diam., strigose. *Bract(s)* 1 (or 2), 1.5–2 by 0.75–1 mm, strigose outside, glabrous inside; bracteole ?. *Sepals* 1–1.5 by 0.75–1 mm, 0.1–0.2 mm thick, strigose outside, glabrous inside. *Inner petals* 1.5 by 0.6–0.7 cm, 0.5 mm thick, margins, base and apex strigose outside, glabrous except margins white puberulous inside. *Torus* 2 mm wide, 2 mm high, sparsely strigose. *Stamens* 60–65, 1.5–2 mm long, 0.75–1 mm wide at the apex, 0.33–0.5 mm wide at the base; connective prolongation not covering thecae; thecae 1 by 0.2 mm. *Carpels* 25, 1.5–2 by 0.5–0.75 mm; style 0–5 mm long, stigma sessile, 0.5–0.75 by 0.33–0.5 mm, margins and top cobwebbed; ovule(s) 1, sublateral (between middle and base). No monocarps seen.

Distribution — Malaysia: Sabah.

Habitat & Ecology — Flowering: Dec. (semi-mature flowers).

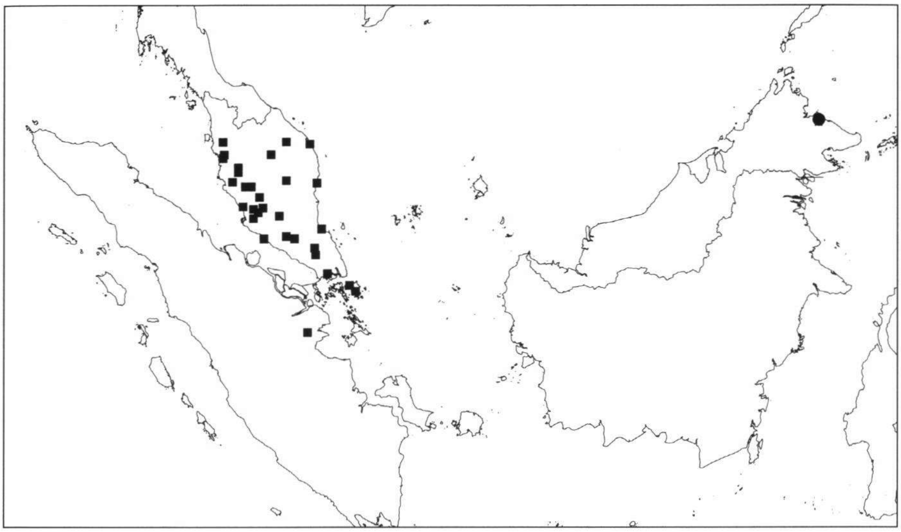
Field note — Indument colour rusty or chestnut-brown (or ochre).

Note — Only type collection known. The flowers are relatively young, so the stamens, carpels etc. are not fully grown and all the flower measurements might be different in mature flowers. The flower resembles the flowers of *Ph. ebracteolatus* except that the connective prolongation does not cover the thecae and that the ovule-placement is lower than usually in *Ph. ebracteolatus*. The most important distinction is the thickness of the leaves and the indument of the flowers.

3. Phaeanthus nutans Hook.f. & Thomson — Map 3

Phaeanthus nutans Hook.f. & Thomson, Fl. Ind. 1 (1855) 147; Miq., Fl. Ned. Ind. 1, 2 (1858) 51; Scheff., Natuurk. Tijdschr. Ned.-Indië 31 (1870) 14; Hook.f. & Thomson in Hook.f., Fl. Brit. India 1 (1872) 72; King, J. Asiat. Soc. Bengal., Pt. 2, Nat. Hist. 61 (1892) 121; Ann. Roy. Bot. Gard. (Calcutta) 4 (1893) 152, pl. 200B; Ridl., Fl. Malay. Penins. 1 (1922) 95; J. Sinclair, Gard. Bull. Straits Settlem. 14 (1955) 374 (sub *Ph. ophthalmicus*); Keng, Gard. Bull. Straits Settlem., ser. 3, 27 (1974) 73 (sub *Ph. ophthalmicus*). — Type: *Wallich 6481* (hololecto K, designated here; isolecto BM), Singapore, fl.

Shrubs or trees, 1–9(–15) m tall, 1.2–10.2(–20) cm diam. *Outer bark* dark grey, glabrous; inner bark brown to white; wood yellow to white. *Old branches* glabrous to sparsely pilose; young branches 1–3 mm diam., pilose; internodes 0.5–3.6 cm long. *Vegetative buds* strigose to pilose. *Petioles* 3–10 mm long, 1–2.5 mm diam., pilose, glabrescent. *Leaves* 8–23 by 2.1–9.7 cm; glabrous above, midrib short to long pilose, midrib and lateral veins pilose below; veins 11–15(–19) pairs, at an angle of 30–50° to the midrib, anastomosing 1–4 mm from the margin. *Cymes* reduced to one axis, 1- or 2-flowered; peduncles 2–8(–13) mm long, 0.75–1.5 mm diam., pilose; pedicels 1.1–4.2(–9.6) cm long, 0.75–1.75 mm diam., (sparsely) pilose. *Bract(s)* 1 (or 2), (1.75–)4–7(–19) by 0.5–1 mm, appressed pilose outside, sparsely white puberulous inside; bracteole 1, 2–6(–11) by 0.5–1 mm, placed up to halfway the pedicel. *Sepals* 3–9(–13) by 1–2(–3) mm, 0.1–0.2 mm thick, appressed pilose outside and inside, hairs longer near the margin. *Inner petals* 1.6–2.7 by 0.8–1.6 cm, 1 mm thick, with 5–7 prominent veins, veins, base and margins sparsely appressed pilose, veins, apex and margins white puberulous inside. *Torus* 3–4 mm wide, 2–2.5 mm high, strigose.



Map 3. Distribution of *Phaeanthus impressinervius* Merr. (●), *Ph. nutans* Hook.f. & Thomson (■).

Stamens 80–100, 1.25–2.25 mm long, 0.75–1 mm wide at the apex, 0.5 mm wide at the base; thecae 1–1.25 by 0.2 mm. *Carpels* 15–20, 1.5–2 by 0.5–0.6 mm; stigma sessile, 0.75–1.5 by 0.5–0.75 mm, margins and top cobwebbed, glabrescent; ovule(s) 1 (or 2), basilateral. *Monocarps* 4–15, 1.1–1.6(–2.2) cm long, 7–8 mm diam., apex 1–2 mm long, base and apex sparsely strigose; stipe 0.6–1.2(–1.9) cm long, 1–2 mm diam., very or sparsely pilose. *Seed(s)* 1 (or 2), 1.2–1.6 cm by 5–6 mm; monocarp wall 0.33–0.5 mm thick.

Distribution — Sumatra, Riau, Peninsular Malaysia, Singapore.

Habitat & Ecology — Understorey tree in primary or secondary lowland forests and freshwater swamps; on steep hills especially on ridges and on riversides; on granite boulders, clay or sandy soil. Altitude 60–610 m. Flowering: May to July, Sep. to Dec. Fruiting: Feb., Apr., Aug. to Nov.

Field notes — Leaves above shiny green, below sea-green. Flowers yellow to cream when mature; with apple-like smell. Monocarps dark red to purple when mature. Indument colour rusty or ochre (or chestnut brown).

Note — When Hooker Jr. & Thomson (1855) established the genus and this species they mentioned that this species is identical to *Uvaria ophthalmica* Roxb. ex G. Don [Gen. Hist. 1 (1831) 93] and *Uvaria tripetala* Roxb. [Fl. Ind. 2 (1832) 667]. They did not indicate that they studied the type specimen that Roxburgh used for the protologue. Sinclair (1955) mentioned that the correct name for *Ph. nutans* should be *Ph. ophthalmicus* because one has to use the oldest epithet. Like Hooker Jr. & Thomson, Sinclair only mentioned that he had the description of Roxburgh at hand and not the type specimen. There is no certainty based on the description that the plant described by Roxburgh belongs to *Phaeanthus* (it could also be a *Miliusa*). Forman (1997) also was not able, after studying both the Roxburgh manuscripts and the Wallich Herbarium, to designate a type for *Uvaria ophthalmica*. He did indicate that together with the manuscripts of Flora Indica, drawings were made of some of the plants described by Roxburgh. The drawing of *Uvaria tripetala* (name used by Roxburgh) might have been used by Sinclair as type specimen. But after examining the drawing (nr. 2292 in Roxburgh's list) we cannot conclude it is a *Ph. nutans*. It does appear to be a *Phaeanthus*, but some of the features drawn resemble one species, while other features resemble another species. We therefore think that *Ph. nutans* should be reinstated and that *Ph. ophthalmicus* J. Sinclair (1955) should be considered a nomen dubium. According to the protologue the type specimen originates from the Moluccas; however, no material from the Moluccas could be identified as this species. Most probably Roxburgh used a plant cultivated at the Botanical Gardens in Calcutta for his description.

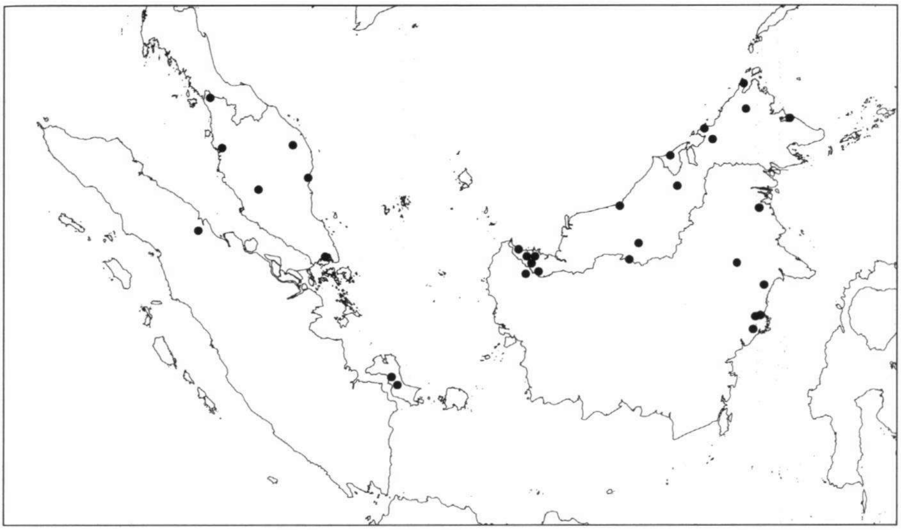
4. Phaeanthus splendens Miq. — Map 4

Phaeanthus splendens Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1865) 40; Ridl., Sarawak Mus. J. 1, 3 (1913) 88; Van Heusden & Keßler, Rheedea 3, 1 (1993) 75. — Type: *Korthals s.n.* (holo L barcode 0045058; iso A, B, L barcode 0045059, U), Borneo, G. Sakoembang, fr.

Phaeanthus crassipetalus Becc., Nuovo Giorn. Bot. Ital. 3 (1871) 191; Scheff., Natuurk. Tijdschr. Ned.-Indië 34 (1874) 85; Ridl., Sarawak Mus. J. 1, 3 (1913) 88; J. Sinclair, Gard. Bull. Straits Settlem. 14 (1955) 376, syn. nov.— Type: *Beccari PB 2508* (holo FI, n.v.; iso A, B, BO, K, P), Borneo, fl.

Phaeanthus lucidus Oliv., Hooker's Icon Pl. (1887) pl. 1561; King, J. Asiat. Soc. Bengal., Pt. 2, Nat. Hist. 61 (1892) 121; Ann. Roy. Bot. Gard. (Calcutta) 4 (1893) 152, pl. 200A; Ridl., Fl. Malay. Penins. 1 (1922) 96. — *Miliusa lucida* (Oliv.) Finet & Gagnep., Bull. Soc. Bot. France 53, Mém. 4 (1906) 151, syn. nov. — Type: *Curtis 839* (hololecto K, designated here; isolecto SING), Malaysia, Peninsular Malaysia, Penang, Waterfall, fl.

Shrubs or trees 3.5–24.5 m tall, 7–29 cm diam.; buttresses sometimes present. *Outer bark* dark grey or brown-black, glabrous; inner bark brown to ochre; wood yellow to white. *Old branches* glabrous to sparsely strigose; young branches 1–4 mm diam., (sparsely) strigose; internodes 0.5–3.4 cm long. *Vegetative buds* strigose. *Petioles* 4–10 mm long, 1–2 mm diam., strigose, glabrescent. *Leaves* 8.5–23.6 by 2.5–9.2 cm; glabrous, midrib short to long pilose or strigose above, midrib and lateral veins sparsely strigose below; veins 9–13(–16) pairs, at an angle of 25–45° to the midrib, anastomosing 1–3 mm from the margin. *Cymes* reduced to one axis, 1–3-flowered; peduncles 1–4(–7) mm long, 1–2 mm diam., strigose, glabrescent; pedicels 1.2–4.9 cm long, 0.75–1.25 mm diam., (sparsely) strigose. *Bract(s)* 1 (or 2), 1.25–2.5 by 0.75–1.25 mm, strigose outside, glabrous inside; bracteole 1, 1–2 by 0.75–1.5 mm, placed quarter- to halfway the pedicel. *Sepals* 1–2 by 1.5–2.25 mm, 0.2 mm thick, strigose outside, glabrous inside. *Inner petals* 0.9–1.7(–2.6) by 0.6–0.9 cm, 1.5–2.25 mm thick, coriaceous, margins, base and apex strigose outside, apex and margins white puberulous inside. *Torus* 2.5–3.5 mm wide, 1.5–2.5 mm high, strigose. *Stamens* 60–90, 1–2 mm long, 0.75–1 mm wide at the apex, 0.5 mm wide at the base; connective prolongation not spread over edge and thecae; thecae 0.75–1 by 0.2–0.25 mm. *Carpels* 30–50, 1–1.75 by 0.5–0.75 mm; stigma sessile, 0.75–1.5 by 0.33–0.66 mm, margins and top cobwebbed, glabrescent; ovule(s) 1 (or 2), lateral. *Monocarps* (2–)6–15, 1.9–3 cm long, 1.1–1.4 cm diam., apex 1–3 mm long, base and apex sparsely strigose; stipe 1.3–3.3 cm long, 1–2 mm diam., sparsely strigose, glabrescent. *Seed(s)* 1 (or 2), 1.3–2.2 by 1–1.2 cm; monocarp wall 0.75–1 mm thick.



Map 4. Distribution of *Phaeanthus splendens* Miq.

Distribution — Sumatra, Bangka, Peninsular Malaysia, Singapore, Sarawak, Brunei, Sabah, Kalimantan.

Habitat & Ecology — Understorey tree in primary or secondary lowland forests and freshwater swamps; on steep hills, especially on ridges; on yellow clay, rocky, sandy, loamy or limestone soil. Altitude 35–540 m. Flowering: Apr. to June, Sep. to Dec. Fruiting: Jan., Mar. to July, Oct. to Dec.

Field notes — Leaves above very shiny green, below (olive) green. Flowers yellow to cream when mature. Monocarps dark red to purple when mature. Indument colour rusty or ochre (or chestnut-brown).

Note — Several collections of the species have a strange appearance and are quite atypical. Collections *S 26947*, *KEP/FRI 11845* and *King's collector 7275* have very small monocarps. *Simpson 2148* has a very atypical flower, there are four inner petals and these are thin. In the protologue of *Ph. lucidus* the type was mentioned as a collection made by Curtis without number, however with location and altitude (Penang, 500 ft). Of all collections studied only *Curtis 839* had this location and altitude.

5. Phaeanthus sumatrana Miq. — Map 5

Phaeanthus sumatrana Miq., Fl. Ned. Ind., Eerste Bijv. 1 (1861) 382; Scheff., Natuurk. Tijdschr. Ned.-Indië 31 (1870) 14. — Type: *Diepenhorst HB 3100* (holo U; iso BO), Sumatra occid v.c. in districtu Priaman, fl. & fr.

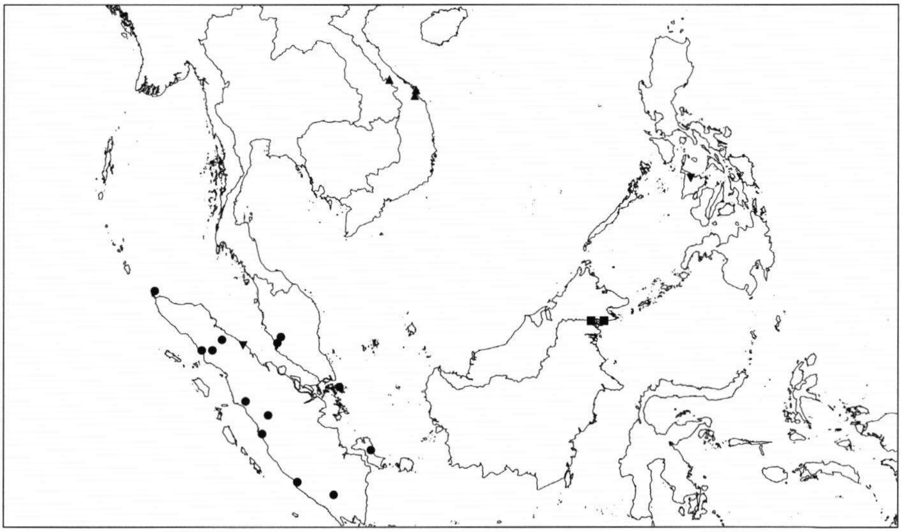
Shrubs or treelets, 1.5–7 m tall. *Old branches* glabrous to (sparsely) pilose; young branches 1–4 mm diam., pilose; internodes 0.2–4 cm long. *Vegetative buds* pilose to slightly strigose. *Petioles* 3–7 mm long, 0.75–2 mm diam., pilose, glabrescent. *Leaves* 10.1–25.9 by 3.9–9.1 cm; glabrous above, midrib short to long pilose, midrib and lateral veins (seldom sparsely) pilose below; veins (13–)15–19 pairs, at an angle of 30–50° to the midrib, anastomosing 1–5 mm from the margin. *Cymes* reduced to one axis, 1- or 2-flowered; peduncles 4–8(–12) mm long, 0.75–1 mm diam., pilose; pedicels 1–5.4(–9.2) cm long, 0.75–1 mm diam., (sparsely) pilose. *Bract(s)* 1 (or 2), 1.5–5 by 0.75–1.25 mm, pilose outside, appressed sparsely pilose inside; bracteole 1, 0.75–2 by 0.75–1.25 mm, placed up to halfway the pedicel. *Sepals* 1.25–4 by 0.75–2 mm, 0.1–0.2 mm thick, appressed pilose outside, appressed pilose to glabrous inside; in younger flowers the outer petals seem longer than the sepals, not in mature ones. *Inner petals* 1.3–2.2(–3.3) by 0.9–1.3 cm, 0.5–0.75 mm thick, with 4–6 veins, veins, apex and margins sparsely (appressed) pilose outside, apex and margins white puberulous inside. *Torus* 3–4 mm wide, 1.5–2 mm high, strigose. *Stamens* 75–110, 1.25–2.5 mm long, 0.75–1.5 mm wide at the apex, 0.33–0.5 mm wide at the base; thecae 0.75–1.25 by 0.2 mm. *Carpels* 25–35, 1.5–2.75 by 0.5–0.75 mm; stigma sessile, 0.75–1.5 by 0.66–0.75 mm, margins and top cobwebbed, glabrescent; ovule(s) 1 (or 2), lateral. *Monocarps* (5–)15–25, 1.3–1.8 cm long, 7–10 mm diam., apex 0.5–1 mm long, base and apex sparsely strigose; stipe 1.2–2.4 cm long, 1–1.5 mm diam., very or sparsely pilose, glabrescent. *Seed(s)* 1 (or 2), 1.2–1.5 cm by 5–8 mm; monocarp wall 0.2–0.5 mm thick.

Distribution — Sumatra, Riau, Peninsular Malaysia, (Java, cultivated).

Habitat & Ecology — Understorey (rare) tree in primary or secondary lowland forests; on sloping hills and on riversides; on yellow-red loamy, clay, sandy or basalt rock soil. Altitude 60–600 m. Flowering: Mar. to Aug., Oct. Fruiting: Feb. to Aug.

Field notes — Leaves above dark green, below sea-green. Flowers yellow to cream when mature, inside purple-green. Monocarps dark red to purple when mature; stipes carmine red. Indument colour rusty or ochre (or chestnut-brown).

Note — All material cited occurring in Java were collected from Botanical Garden trees in Bogor. Their original occurrence could not be traced so far. Only two collections from Peninsular Malaysia (c. 30 from Sumatra).



Map 5. Distribution of *Phaeanthus sumatrana* Miq. (●), *Ph. tephrocarpus* Merr. (■), *Ph. vietnamensis* Bân (▲), and *Ph. villosus* Merr. (▼).

6. Phaeanthus tephrocarpus Merr. — Map 5

Phaeanthus tephrocarpus Merr., Univ. Calif. Publ. Bot. 15 (1929) 68. — Type: *Elmer 21860* (holo PNH†; iso A, B, BM, BO, K, L, P, U, UC, US), Malaysia, Sabah, Elphinstone Prov., Tawau, fr.

Shrubs or trees, 7.6 m tall. *Outer bark* dark yellow, glabrous; inner bark yellow; wood yellow. *Old branches* glabrous to (sparsely) pilose; young branches 1–4 mm diam., pilose; internodes 1–2.9 cm long. *Vegetative buds* pilose. *Petioles* 4–8 mm long, 1.25–2 mm diam., pilose, glabrescent. *Leaves* 7.4–25.2 by 3–7.9 cm; glabrous above, midrib short to long pilose, midrib and lateral veins pilose below; veins 11–15 pairs, at an angle of 30–45° to the midrib, anastomosing 0–1.5 mm from the margin. No flowers seen. In fruit: *Peduncles* 6–7 mm long, 1.5–2.25 mm diam., pilose, glabrescent; pedicels 2.9–3.5 cm long, 1.5–3.5 mm diam., pilose, glabrescent. *Bract(s)* 1 (or 2) broken off; bracteole ?. *Sepals* and *outer petals* persistent in fruit; sepals 2.5–3.25 by 1.75–2.5 mm, 0.2–0.3 mm thick, appressed pilose outside and inside. *Torus* 10–20 mm wide, 10–17 mm high. *Monocarps* 35–60, 1.8–2.2 cm long, 1.1–1.2 mm diam., apex 1–2 mm long, base and apex (sparsely) strigose. *Young monocarps* very puberulous; stipe 2–2.6 cm long, 1.5–2 mm diam., very or sparsely pilose. *Seed(s)* 1 (or 2), 1.6–2.0 cm by 8–9 mm; monocarp wall 0.8–1 mm thick.

Distribution — Malaysia: Sabah.

Habitat & Ecology — Fruiting: Oct. (young monocarps).

Field note — Indument colour chestnut-brown or ochre (or rusty).

Note — Only two collections of the species are available. The typical *Phaeanthus* monocarps are separate from the branches, but according to notes on the UC specimen and Merrill (1929) these monocarps do belong to the vegetative part. The leaves and branches first appeared not even to be Annonaceous (because of their shiny grey colour, they resembled *Dichapetalum* spec. but lack stipules and glands), but a wood anatomical study of the branches revealed that this specimen certainly belongs to the Annonaceae. The monocarps resemble those of *Ph. splendens* in size, but the monocarps of *Ph. tephrocarpus* are puberulous and are present in a higher number. Additionally, the leaves of *Ph. splendens* are sparsely covered by strigose hairs or are totally glabrous, while those of *Ph. tephrocarpus* are covered by pilose hairs.

7. Phaeanthus vietnamensis Bân — Map 5

Phaeanthus vietnamensis Bân, Fl. Vietn. 1 (2000) 170; J. Biol. (Vietnam) 16, 4 (1994) 11, nom. nud. — Type: *Thai Thuan 8* (holo HN, iso LE), Vietnam, Thua Thien Hue, Phu Loc, Rung Nong, fl.

Shrubs or trees, 2–10 m tall, 15 cm diam. *Old branches* glabrous to sparsely strigose; young branches 1–3.5 mm diam., sparsely strigose; internodes 1–4.6 cm long. *Vegetative buds* strigose. *Petioles* 3–10 mm long, 0.75–2 mm diam., strigose, glabrescent. *Leaves* 4.8–20.7 by 2.1–7.3 cm; glabrous, midrib sparsely short to long pilose or strigose above, midrib and lateral veins sparsely strigose below; veins 10–14 pairs, at an angle of 30–50° to the midrib, anastomosing 1–4 mm from the margin. *Cymes* reduced to one axis, 1-flowered; peduncles (4–)10–15 mm long, 0.5–0.75 mm diam., strigose, glabrescent; pedicels 0.3–3 cm long, 0.5–1 mm diam., (sparsely) strigose. *Bract(s)* 1 (or 2), 1–4 mm long with the lowest bract the longest, 0.25–1.25 mm wide, appressed rusty strigose outside, glabrous inside; bracteole 1, 0.75–2 by 0.5–1 mm, placed up to halfway the pedicel. *Sepals* 1–2 by 0.75–1.25 mm, 0.1–0.2 mm thick, strigose outside, glabrous inside. *Inner petals* 0.7(young)–1.2 by 0.4(young)–0.6 cm, 0.5–0.75 mm thick, margins, base and apex strigose outside, 4–6 veins visible when boiled, apex and margins white puberulous inside. *Torus* 2 mm wide, 1.5 mm high, rusty strigose. *Stamens* 80–95, 1.25–2 mm long, 0.75–1.25 mm wide at the apex, 0.33–0.5 mm wide at the base; thecae 1–1.25 by 0.2 mm. *Carpels* 10–20, 1.75–2 by 0.5–1 mm; stigma sessile, 0.66–1 by 0.33–0.5 mm, margins and top cobwebbed, glabrescent; ovule(s) 1 (or 2), lateral. *Monocarps* (2–)10–20, 1.2–1.8(–2.2) cm long, 6–9 mm diam., apex 0.5–1 mm long, base and apex sparsely strigose; stipe 1.1–2.4 cm long, 1.5–1.75 mm diam., (sparsely) strigose. *Seed(s)* 1 (or 2), 0.9–1.7 cm by 5–7 mm; monocarp wall 0.25–0.33 mm thick.

Distribution — Vietnam.

Habitat & Ecology — Primary forest; on clay or rocky soil. Altitude 600 m. Flowering: Jan., Mar., Aug. Fruiting: June to Aug.

Field note — Indument colour rusty (or chestnut-brown or ochre).

8. Phaeanthus villosus Merr. — Map 5

Phaeanthus villosus Merr., Philipp. J. Sci. 14 (1919) 391; Enum. Philipp. Fl. Pl., 2 (1923) 165. — Type: *BS 30775 (Ramos & Edaño)* (holo PNH†; iso A, B, BM, BO, K, L, P), Philippines, Panay, Capiz Prov. Mt Macosolon, fl.

Shrubs. *Old branches* glabrous to sparsely pilose; young branches 1–3 mm diam., pilose; internodes 1.1–4 cm long. *Vegetative buds* pilose. *Petioles* 5–10 mm long, 1.5–2.25 mm diam., pilose, glabrescent. *Leaves* 13.1–22 by 4.6–7.4 cm; glabrous above, midrib short to long pilose, midrib and lateral veins pilose below; veins 16–20 pairs, at an angle of 30–45° to the midrib, anastomosing 1–2 mm from the margin. *Cymes* reduced to one axis, 1- or 2-flowered; peduncles 9–22 mm long, 0.75–1 mm diam., pilose, glabrescent; pedicels 6.5–7.7 cm long, 0.75–1 mm diam., pilose. *Bract(s)* 1 (or 2), 1.5–3 by 0.75–1 mm, appressed pilose to strigose outside, glabrous inside; bracteole 1, 0.75–1.5 by 0.5–0.75 mm, placed up to 2/10 from base of the pedicel. *Sepals* 1–1.75 by 1.25–1.75 mm, 0.1–0.2 mm thick, appressed pilose to strigose outside, glabrous inside. *Inner petals* 2.5–3.7 by 1–1.3 cm, 0.75 mm thick, margins, base, veins and apex pilose outside, 4–6 veins visible when boiled, glabrous inside. *Torus* 3.5–4 mm wide, 2–3 mm high, pilose to strigose. *Stamens* 75–80, 2.25–3 mm long, 0.75–1 mm wide at the apex, 0.33–0.66 mm wide at the base; thecae 1.25–2 by 0.2 mm. *Carpels* 40–50, 1.75–2.5 by 0.5–0.75 mm; stigma sessile, 1–1.5 by 0.33–0.75 mm, margins and top cobwebbed, glabrescent; ovule(s) 1 (or 2), lateral.

Distribution — Philippines: Panay.

Habitat & Ecology — Flowering: April.

Field note — Indument colour rusty or ochre (or rose).

Note — Only one collection studied. The leaves and flowers resemble *Ph. ebracteolatus*. *Phaeanthus villosus* differs from *Ph. ebracteolatus* in having very long pedicels and leaves having many more secondary veins. Additionally the leaves are thinner. There is no transition between the two species and therefore both should retain species status.

DUBIOUS SPECIES

Phaeanthus ophthalmicus (Roxb. ex G. Don) J. Sinclair, Gard. Bull. Straits Settlem. 14 (1955) 374. — *Uvaria ophthalmica* Roxb. ex G. Don, Gen. Hist. 1 (1831) 93. — *Uvaria tripetala* Roxb. non Blanco, non Lam., Fl. Ind. 2 (1832) 667. — *Phaeanthus nutans* Hook.f. & Thomson, Fl. Ind. 1 (1855) 147.

We were unable to trace the type specimen for this species. Neither Sinclair (1955) nor Hooker Jr. & Thomson (1855) mentioned which specimen they used as type specimen (also confer notes under *Ph. nutans*). When examining Roxburgh drawing nr. 2292 this appears to be a *Phaeanthus*, but it is not clear to which species this specimen might belong.

EXCLUDED SPECIES

Phaeanthus acuminatus Merr., Bureau of Government Laboratories 35 (1906) 11. — Type: *Merrill 4050* (holo PNH†; iso B, P), Philippines, Mindoro, Baco River.
This specimen probably is a **Polyalthia**.

Phaeanthus andamanicus King, J. Asiat. Soc. Bengal Pt. 2, Nat. Hist. 61 (1893) 122. — Type: *King's collector s.n.* (holo CAL, n.v.), India, South Andaman = **Miliusa andamanica** (King) Finet & Gagnep., Bull. Soc. Bot. France 53, Mém. 4 (1906) 151.

Phaeanthus dioicus (Roxb.) Kurz, Flora 53 (1870) 274. — *Uvaria dioica* Roxb., Fl. Ind. 2 (1832) 659. — Type: *Roxburgh s.n.* (holo CAL, n.v.), Bangladesh, Sylhet = **Miliusa globosa** (A.DC.) Panigrahi & S.C. Mishra, Taxon 33, 4 (1984) 713.

Phaeanthus glabrescens (Oliv.) Baill., Hist. Pl. 1 (1868) 246. — *Piptostigma glabrescens* Oliv., J. Linn. Soc. 8 (1865) 159. — Type: *Mann 1792* (holo P, n.v.), Gabon, Kongui River = **Piptostigma glabrescens** Oliv., J. Linn. Soc. 8 (1865) 159.

Phaeanthus heteropetalus (Benth.) Baill., Hist. Pl. 1 (1868) 245. — *Heteropetalum brasiliense* Benth., J. Linn. Soc. 5 (1861) 69. — *Guatteria heteropetala* Benth., Hook. Journ. 2 (1843) 360. — Type: *Schomburgk 950* (holo K, n.v.), Brazil, Rio Negro = **Heteropetalum brasiliense** Benth., J. Linn. Soc. 5 (1861) 69.

Phaeanthus lanceolatus Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1865) 40. — Syntypes: *De Vriese s.n.* (L, U).
Not *Phaeanthus*, probably **Goniothalamus**.

Phaeanthus malabaricus Bedd., Icon. Pl. Ind. Or. 1 (1874) 16, t. 76. — Type: *Beddome s.n.* (holo K, n.v.), India, South Wynaad, abundant in the forests of the Tambacherry ghat about 2000 ft elevation = **Polyalthia suberosa** (Roxb.) Thwaites, Enum. Pl. Zeyl. (1864) 398.

Phaeanthus moulmeinensis Craib, Feddes Repert. 12 (1913) 392. — Type: *Meebold 17249* (holo K), Birma, Moulmein, Mizar = **Polyalthia rufescens** Hook.f. & Thomson, Fl. Brit. India 1 (1872) 66.
According to Sinclair mss (held at L) *Polyalthia rufescens*. Type could be *Polyalthia*.

Phaeanthus pilosus (Oliv.) Baill., Hist. Pl. 1 (1868) 246. — *Piptostigma pilosum* Oliv., J. Linn. Soc. 8 (1865) 159. — Type: *Thomson 61* (holo K, n.v.), Nigeria, Old Calabar = **Piptostigma pilosum** Oliv., J. Linn. Soc. 8 (1865) 159.

Phaeanthus saccopetaloides W.T. Wang, Acta Phytotax. Sin. 6 (1957) 199. — Type: *T.T. Yu 17336* (holo PE, n.v.), China, Yunnan, Mang-lung.
Not a *Phaeanthus*, maybe **Miliusa**. Type not seen but paratype *T.T. Yu 16484*.

Phaeanthus yunnanensis Hu, Bull. Fan Mem. Inst. Biol. 10 (1940) 125. — Type: *C.W. Wang 19167* (holo PE, n.v.), China, Yunnan, Che-Li Hsien, Jah-Leei = **Dasymaschalon yunnanense** (Hu) Bân, Bot. Zhurn. 60 (1975) 230.
Type not seen but paratype *C.W. Wang 77921*.

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IDENTIFICATION LIST

The numbers behind the collections refer to the species numbers as given in the key and descriptions above. When the number of the collection is not available or unknown then dates or sheet numbers are mentioned between brackets (when no sheet number is known, the herbarium is mentioned with collecting location). The collections from institutions can be found under the abbreviation of the institution (the collectors are mentioned between brackets).

Phaeanthus	5. *sumatrana*
1. *ebracteolatus*	6. *tephrocarpus*
2. *impressinervius*	7. *vietnamensis*
3. *nutans*	8. *villosus*
4. *splendens*	9. spec.

Abu Kassim 281: 3 — Aet 294: 1 — Ahamad C7-2485: 4 — Alston 16450: 1 — Ambri & Arifin AA 496: 4; W 727: 4; W 997: 4 — Ambriansyah & Arbainsyah AA 1442: 4 — Amiruddin 9: 3 — Anthonysamy SA 954: 4 — Arbainsyah et al. AA 1982: 4 — Arifin & Arbainsyah AA 1823: 4 — Atasrip 65: 1 — Atjeh 232: 1.

Bartlett 14326: 1 — Beccari PB 2508: 4; PB 2788: 9; PB 3048: 4; PP s.n. (1872): 1; PS 550: 5 — Bloembergen 4320: 1 — Brass 29248: 1 — BRUN 3012 (Ashton): 4; 15040 (Nangkat, Joffre & Arifin): 1; 15463 (Joffre, Hussain, Suhaili, Jangarun & Talip): 4 — BS 1607 (Foxworthy): 1; 1792 (Ramos): 2; 3355 (Ramos): 1; 4057 (Fenix): 1; 6856 (Robinson): 1; 15200 (Ramos): 1; 22092 (Ramos): 1; 23477 (Ramos): 1; 23859 (Ramos): 1; 26230 (Ramos & Edaño): 1; 26437 (Ramos & Edaño): 1; 27333 (Ramos): 1; 29265 (Ramos & Edaño): 1; 30775 (Ramos & Edaño): 8; 32815 (Ramos): 1; 33081 (Ramos): 1; 33590 (Ramos & Edaño): 1; 33891 (Ramos & Edaño): 1; 35469 (Martelino & Edaño): 1; 39527 (Ramos): 1; 39709 (Ramos): 1; 39815 (Ramos): 1; 40908 (Ramos): 1; 40919 (Ramos): 1; 43091 (Ramos): 1; 43364 (Ramos): 1; 44050 (Ramos &

Edaño): 1; 44536 (Ramos): 1; 44752 (Ramos & Edaño): 1; 46371 (Ramos): 1; 46591 (Ramos & Edaño): 1; 46644 (Ramos & Edaño): 1; 47238 (Ramos & Edaño): 1; 48042 (Ramos & Edaño): 1; 48059 (Ramos & Edaño); 1; 48102 (Ramos & Edaño): 1; 48252 (Ramos & Edaño): 1; 48472 (Ramos & Edaño); 1; 49388 (Ramos & Edaño): 1; 75121 (Ramos & Edaño): 1; 75358 (Ramos & Edaño): 1; 76130 (Edaño): 1; 76142 (Edaño): 1; 76448 (Edaño): 1; 78342 (Edaño): 1 — Burkill HMB 4550: 3 — Burley 181: 1 — BW 709 (Versteegh): 1; 4333 (Koster): 1; 4667 (Versteegh): 1; 5993 (Schram): 1; 11083 (Koster): 1; 12125 (Vink): 1; 14854 (Schram): 1.

Chew Wee Lek & Noor CWL 274: 3 — Clemens & Clemens 3513: 7; 4237: 7 — Coode 5428: 1 — Cuming 525: 1; 1084: 1 — Curran 342: 1 — Curtis 839: 4; 1407: 4; 1416: 3; s.n. (5-1894): 4.

David 42: 3; 223: 4 — De Vogel 1068: 1; 1316: 5; 2558: 1 — De Vriese s.n. (L 0046163): 5 — De Wilde & De Wilde Duyfjes 18774: 5; 18801: 5; 19662: 5; 19875: 5; 21286: 5 — Diepenhorst 13982: 5; HB 2227: 5; HB 2355: 9; HB 3100: 5 — Dransfield JD 7058: 1.

Elbert 4116: 9 — Elmer 6679: 1; 13727: 1; 15168: 1; 17183: 1; 20956: 1; 21860: 6.

Fallen, Lelean & Franklin 336a: 1 — FB 64 (Whitford): 1; 159 (Barnes): 1; 179 (Ahern's collector): 1; 1030 (Whitford): 1; 1204 (Borden): 1; 1418 (Ahern's collector): 1; 1481 (Ahern's collector): 1; 1491 (Ahern's collector): 1; 1690 (Borden): 1; 1750 (Borden): 1; 2179 (Meyer): 1; 3022 (Meyer): 1; 3343 (Ahern's collector): 1; 13375 (Alvarez): 1; 14850 (Darling): 1; 14873 (Darling): 1; 17275 (Curran): 1; 20045 (Topacio): 1; 22092 (Paraiso): 1; 22861 (Medina): 1; 23272 (Velasco): 1; 23538 (Medina): 1; 24091 (Barros): 1; 24555 (Sulit): 1; 24566 (Baldemor): 1; 26100 (Oliveros): 1; 26316 (Mabesa): 1; 26858 (De Guzman): 1; 28525 (Cenabre et al.): 1; 29157 (Cenabre): 1; 29982 (Cenabre): 1 — FMS see KEP/FRI — Forbes 2911: 5 — Forman 230: 1 — Fox s.n. (10-1890): 4 — FRI see KEP/FRI.

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