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The rise and fall of Sauropus (Phyllanthaceae) : a molecular phylogenetic analysis of Sauropus and allies

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Sauropus transferred to *Breynia* (Phyllanthaceae) based on molecular and morphological phylogenetic reconstruction^{*},[@]

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Abstract

Phylogenetic analyses of *Sauropus* sensu stricto (i.e., excluding *Synostemon*) and allied genera, based on molecular and morphological data, find that *Breynia* and *Sauropus* form a monophyletic group. *Breynia*, the older name, is nested within *Sauropus*, leading us to transfer the latter to *Breynia*. Within this broadened *Breynia*, two subgenera and two sections are distinguished. *Breynia* subgen. *Sauropus* generally has larger leaves, often compound inflorescences, horizontal anthers, and lacks a marginal rim on top of the flattened ovary; *Breynia* subgen. *Breynia* has smaller leaves, horizontal to ascending to vertical stamens, and the stigmas, especially of the former species of *Sauropus*, have a rim. The latter subgenus can be divided into *Breynia* sect. *Cryptogynium* with horizontal to ascending anthers and an ovary with a rim, and section *Breynia* with vertical anthers and the ovary normally without a rim.

^{*} In review for Taxon. [@] The new combinations will officially be made in Taxon, not in this thesis. Therefore, when applicable the name *Sauropus* is still used as much as possible.

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Introduction

Sauropus Blume sensu stricto (excluding *Synostemon* F. Muell.; Pruesapan et al., 2008; Chapters 2 and 3) and *Breynia* J.R.Forst. & G.Forst. are two closely related tropical Asian-Australian genera with up to 83 and 35 species, respectively (Webster, 1994; Govaerts et al., 2000; Radcliffe-Smith, 2001). *Sauropus* comprises mainly herbs and shrubs, whereas species of *Breynia* are shrubs and trees. Both genera share attributes including bifid or emarginate styles, non-apiculate anthers, and generally possessing sepal scales. However, they differ in features of their seed coat, staminate calyx, and androecium (Webster, 1994; Radcliffe-Smith 2001). The staminate flowers have often been used to characterize species in *Sauropus*, whereas the pistillate organs have mainly been used in *Breynia*.

The close relationship between *Breynia* and *Sauropus* was already noted by several authors (Croizat, 1940; Airy Shaw, 1980b, 1981), but they never united the genera. The last complete revision of *Breynia* was made by Müller (1863, 1866), and the last revision of *Sauropus* dates back to Pax & Hoffmann (1922). Since then, only regional accounts of these genera have been published (Table 4.1).

The taxonomic histories of *Breynia* and *Sauropus* are closely linked. Beille (1925) described the genus *Breyniopsis*, which he considered to be related to *Breynia*, while Croizat (1940) remarked that its resemblance to *Sauropus* was much greater, and he transferred *Breyniopsis* to *Sauropus* and stated that the limits between *Breynia* and *Sauropus* are ill defined; as was the case in recent molecular studies (Kathriarachchi et al., 2006; Pruesapan et al., 2008).

Müller Argoviensis (1863, 1866) was the first to describe three sections within *Sauropus* based mainly on floral characters: *S.* sect. *Cryptogynium* ('*Ceratogynium*'), *S.* sect. *Hemisauropus*, and *S.* sect. *Sauropus* ('*Eusauropus*'). Later, Hooker (1887) used Müller Argoviensis' classification for India, where only *S.* sect. *Cryptogynium* and *S.* sect. *Sauropus* occur. Pax & Hoffmann (1922) created the most extensive infrageneric classification with two subgenera, *S.* subgen. *Hemisauropus*, and *S.* subgen. *Sauropus* ('*Holosauropus*'), the latter with five sections: *S.* sect. *Cryptogynium* ('*Ceratogynium*'), *S.* sect. *Retroversi*, *S.* sect. *Sauropus* ('*Eusauropus*'), *S.* sect. *Schizanthi*, and *S.* sect. *Sphaeranthi*. Beille (1927) treated the genus for Indochina preferring the sections of Pax & Hoffman (1922), but not their

subgenera. Airy Shaw (1969), like Beille, dismissed the subgenera, and returned more or less to the classification of Müller Argoviensis, maintaining the four sections of Pax & Hoffmann (1922): *Sauropus* sect. *Cryptogynium*, *S.* sect. *Hemisauropus*, *S.* sect. *Sauropus*, and *S.* sect. *Schizanthi*. He added *S.* sect. *Glochidioidei*. Airy Shaw (1969) combined *S.* sect. *Sphaeranthi* with *S.* sect. *Sauropus* while the monospecific *S.* sect. *Retroversi* was not mentioned by him. *Sauropus retroversus* Wight was considered to be a synonym of *S. androgynus* (L.) Merr. (*S.* sect. *Sauropus*) by Van Welzen (2003). Li (1987) placed all Chinese species of *Sauropus* into *S.* sect. *Sauropus*, except for *S. bacciformis*, which was placed in *S.* section *Synostemon*. Recently, Thin (2007) studied the genus in Vietnam and recognized *S.* subgenus *Sauropus* with *S.* sect. *Cryptogynium*, *S.* sect. *Sauropus*, and *S.* sect. *Schizanthi* and the monotypic *S.* subgen. *Sphaeranthi*. Thin's (2007) placement of several species differs from that by other authors (e.g., *S. bonii*, *S. pierrei*, *S. racemosus*, *S. rhamnoides* and *S. stipitatus* in his *S.* sect. *Sphaeranthi* and *S. villosus* in his *S.* sect. *Cryptogynium*); in our opinion his classification appears to be poorly supported by morphological evidence. The modified classification of Airy Shaw (1969) has been largely accepted by most authors, although there is agreement that some species are difficult to place, or cannot be placed in any existing section (see Van Welzen, 2003).

The molecular phylogenetic reconstruction of *Sauropus* (Pruesapan et al., 2008; Chapter 2) partly agrees with the infrageneric classification of *Sauropus* as proposed by Airy Shaw (1969). Only two out of the five infrageneric groups in *Sauropus* could be recognised within the molecular phylogeny; of these one group forms a clade together with *Breynia* (Pruesapan et al., 2008; Chapters 2 and 3).

DNA sequence data have resolved phylogenetic relationships of numerous plant groups. Yet, the inclusion of morphological data in phylogenetic analysis is necessary, or at least desirable, for the construction of robust estimates of phylogeny (De Queiroz et al., 1995), to have as a "reality check" for molecular results, to resolve the phylogenetic relationships of fossil taxa (Wiens, 2004, and references therein), and to study character evolution (Bremer, 1988). Recently, Sierra et al. (2010) showed that molecular data provided a skeleton phylogeny of *Mallotus* Lour. (Euphorbiaceae), but with additional qualitative and quantitative morphological data a much more resolved phylogeny was obtained. Species of *Sauropus* and *Breynia* appear to form a monophyletic group, with a monophyletic *Breynia* nested within a

paraphyletic *Sauropus* (Kathriarachchi et al., 2006; Pruesapan et al., 2008; Chapters 2 and 3). The group has two clades that split basally, one with a part of *Sauropus* plus *Breynia* and one with only *Sauropus* species. To date, the purely *Sauropus* clade is mainly unresolved (Pruesapan et al. 2008; Chapters 2 and 3). The inclusion of morphological data in phylogenetic analyses is intended to provide better resolved relationships within the group.

Our aims are to (i) clarify the phylogenetic relationships within *Breynia* s.l. (*Breynia* combined with *Sauropus*) based on a combination of molecular and morphological data; (ii) obtain characters useful for the recognition of new infrageneric groups within *Breynia* s.l.; (iii) provide a new classification for *Breynia* s.l. based on monophyletic groups.

Table 4.1. Numbers of species of *Sauropus* s.s. and *Breynia* in different regions of Asia.

Genus	Author(s)	Region	Species
<i>Sauropus</i> s.s.	Beille (1927)	Indochina	22
	Airy Shaw (1969, 1972, 1975, 1981)	SE Asia	17
	Li (1987), Li et al. (2008)	China	14
	Chakrabarty & Gangopadhyay (1996)	India	18
	Van Welzen (2003)	Thailand	28
	Van Welzen (2003)	Malesia	13
	Thin (2007)	Vietnam	23
<i>Breynia</i>	Li (1994), Li et al. (2008)	China	5
	Chakrabarty & Gangopadhyay (1996)	India	4
	Van Welzen & Esser (2000)	Thailand	7
	Thin (2007)	Vietnam	15

Materials and methods

Taxon sampling

The focus of this study is on the relationships within *Sauropus* and *Breynia* (see Pruesapan et al., 2008; Chapters 2 and 3). Twenty six species were selected to represent the sections of *Sauropus* as proposed by Pax & Hoffmann (1922) and Airy Shaw (1969) in combination with representatives of related genera including *Breynia* (nine species), *Glochidion* (five species), *Phyllanthus* (five species), and *Synostemon* (six species). The same species were used to obtain molecular and morphological data. The specimen vouchers,

GenBank accession numbers, list of morphological characters, and morphological data matrix are shown in Appendices 4.1—3.

Molecular and morphological data

The species sampled here were based on sequences of the non-coding *accD-psaI*, *trnS-trnG* and nuclear *PHYC* and ITS that were available from the previous studies (Kathriarachchi et al., 2006, Pruesapan et al., 2008; Chapters 2 and 3). DNA extraction, sequencing, and alignment followed previously described methods in Chapter 3.

The morphological data matrix of *Breynia* and *Sauropus* was constructed using the most recent taxonomic revisions of both genera for Indochina, Malesia, Thailand, and India (Beille, 1925; Chakrabarty & Gangopadhyay, 1996; Van Welzen & Esser, 2000; Van Welzen, 2003; Esser & Stuppy, in prep.). Relevant specimens at the L herbarium were examined for some characters that were not indicated in the literature. The specimens used in the revisions by Van Welzen & Esser (2000), Van Welzen (2003), and Esser & Stuppy (in prep.) were mainly used. The characters of *Synostemon* were taken from Telford et al. (in prep.), and from representative specimens (Appendix 4.1). The characters of *Glochidion* were taken from representative specimens only (Appendix 4.1), the characters of *Phyllanthus* were scored from Chantharanonthai (2007) in combination with specimens (Appendix 4.1), and for the outgroups, we used Vorontsova & Hoffmann (2008) in combination with additional material (Appendix 4.1) for *Notoleptopus decaisnei* (Benth.) Voronts. & Petra Hoffm., while the data of *Flueggea virosa* (Willd.) Voigt were obtained from specimens (Appendix 4.1). All pollen characters were recorded from Sagun & Van der Ham (2003) and Webster & Carpenter (2008).

In total, 20 quantitative and 45 qualitative morphological characters of 54 taxa were coded for the analysis (Appendix 4.3). These morphological characters were used to support the phylogenetic analysis based on molecular markers only. The qualitative data were treated as unordered. The morphological characters were analysed ‘as such’ with TNT (ordered via mean values; Goloboff et al., 2006). The quantitative characters, measured in different scales, were all rescaled to the same range value of 0 to 65 of TNT, and the qualitative characters received a weight of 65.

Phylogenetic analysis

The analyses of the molecular and morphological datasets were conducted under Maximum Parsimony (MP) and Bayesian Inference (BI) following settings previously described in the Material and Methods section of Chapter 3. The MP analyses were run partly using PAUP* v4.0b10 (Swofford, 2003) for the molecular data, and TNT v.1.1. (Goloboff et al., 2003b) for the morphological and molecular data in combination. Polymorphic characters were treated as uncertainties in PAUP, and gaps were treated as missing data. In PAUP, heuristic searches were performed with 10 random addition sequences and tree bisection reconnection (TBR). Bootstrap support was calculated from 1000 bootstrap replicates, holding 10 trees per replicate, with the same settings as the heuristic search. TNT search strategies (Goloboff, 1999; Nixon, 1999) were used to find the most-parsimonious trees (MPTs), with 10--20 initial replicates using TBR. The symmetric resampling (SR) of 1000 replicates (Goloboff et al., 2003a) was run to measure the tree support with each replicate conducting 10 random addition sequence replicates, saving 10 trees per replicate. The SR support was calculated as frequency differences ('GC' values).

Mesquite version 2.72 (build 527) (Maddison & Maddison, 2009) was used to map morphological characters onto the trees of the MP analysis.

Results

DNA sequences

Visual observation showed a high congruence between the main clades between the molecular data only and in the combined molecular and morphological analyses. The latter analyses show a greater resolution but generally with low support for the newly resolved clades

Molecular and qualitative morphological analysis

A total of 3,663 characters, 3,578 nucleotides (ITS, *PHYC*, *accD-psaI*, *trnS-trnG*) and 45 qualitative morphological characters were used, of which 635 are variable and 481 parsimony-informative. The maximum parsimony analysis resulted in 26 most-parsimonious trees (MPTs) of tree length = 2,162, consistency index (CI) = 0.67 (excluding uninformative

characters = 0.52), and retention index (RI) = 0.74. The strict consensus of the 26 shortest trees, with MP bootstrap values, and Bayesian posterior probabilities is shown in Fig. 4.1. The analyses from PAUP* (Fig. 4.1) and TNT (not shown) are largely congruent, but the strict consensus from TNT was somewhat less resolved as species in Clade B formed a polytomy with those of Clade C. The results of the MP and BI analyses returned largely congruent cladograms, but the Bayesian one provided higher overall branch supports. Higher posterior probability values when compared with bootstrap values are normal in this type of analysis (Suzuki et al., 2002).

All cladograms show the same main clades: Representatives of *Phyllanthus* are early divergent, followed by representatives of *Glochidion* being sister to *Phyllanthus mirabilis* Müll. Arg. Next we find the *Synostemon* clade, which forms a sister group to the *Breynia* s.l. clade (Fig. 4.1). The latter clade comprises three monophyletic groups: Clades A and B are made up of species of *Sauropus*, and Clade C includes all species of *Breynia* s.s. Clades A and B are largely unresolved (Fig. 4.1).

Dataset with quantitative characters

The Maximum parsimony analysis run using TNT for the combined datasets including quantitative characters produced only one most parsimonious tree (Fig. 4.2). The symmetric resampling tree (not shown) obtained the same topology as the analysis of molecular and qualitative morphological dataset with species in Clade B of Fig. 4.1 forming a polytomy with Clade C.

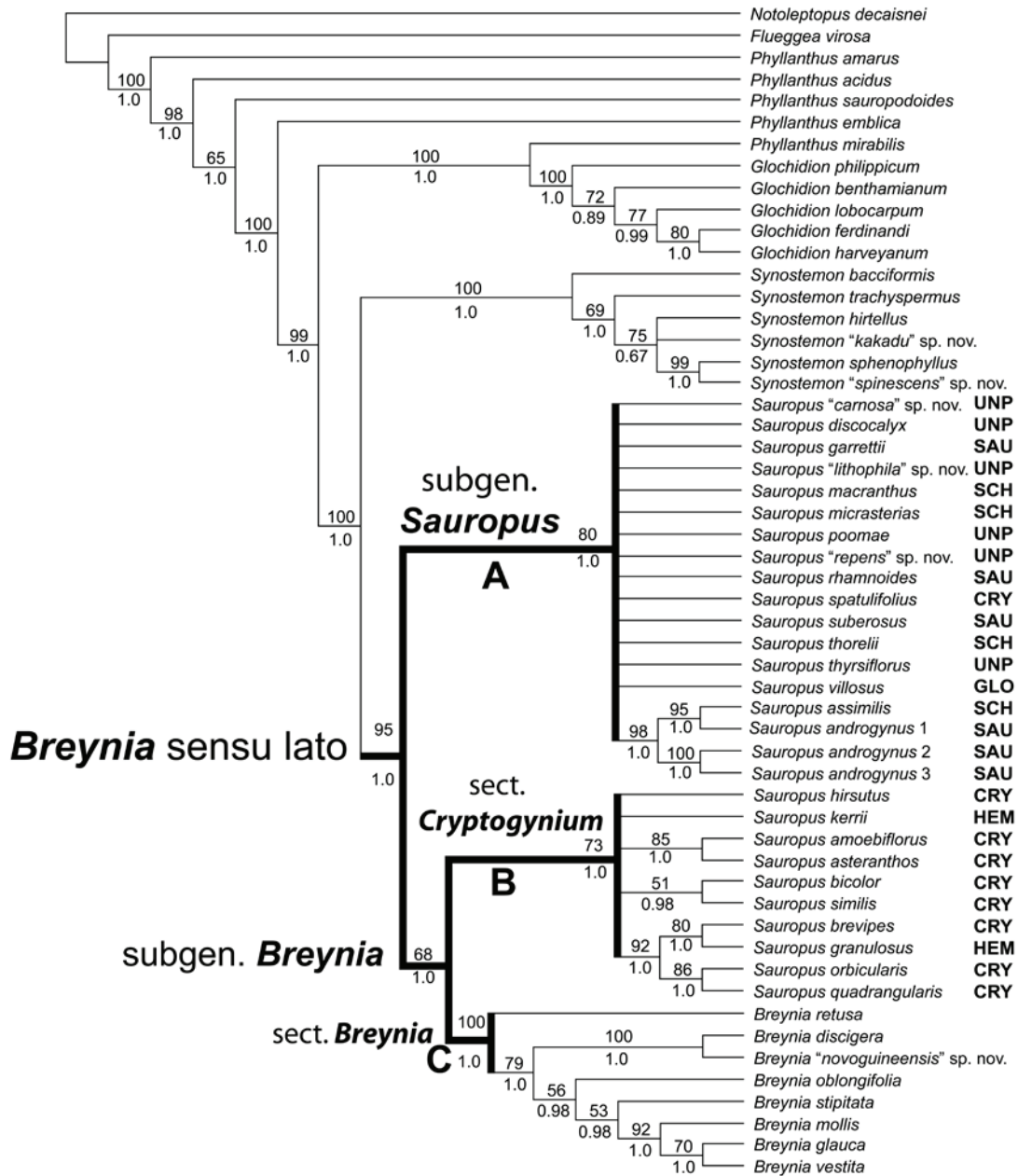


Fig. 4.1. The strict consensus cladogram of the combined molecular and qualitative morphological dataset with bootstrap values (above) and Bayesian posterior probabilities (below; from the Bayesian analysis not shown). Clades A and B include species of *Sauropus* and Clade C consists of species of *Breynia*. Thick lines indicate the subgenera and sections of *Breynia sensu lato*. The abbreviations show the previously recognised sections: CRY = *S. sect. Cryptogynium*, GLO = *S. sect. Glochidioidei*, HEM = *S. sect. Hemisauropus*, SAU = *S. sect. Sauropus*, SCHI = *S. sect. Schizanthi*, and UNP = unplaced species. See text for discussion

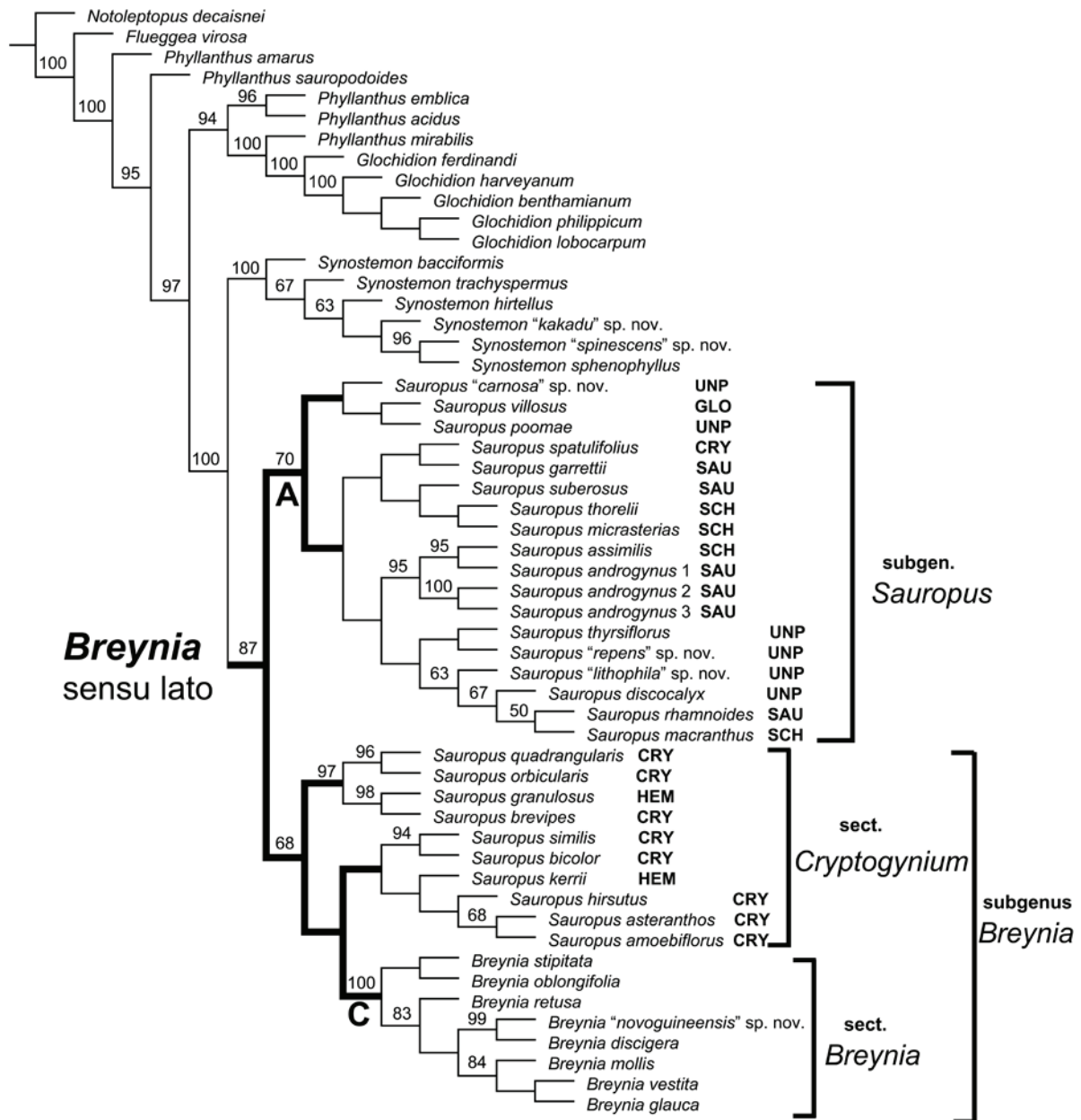


Fig. 4.2. The most parsimonious cladogram of the combined molecular, qualitative and quantitative morphological analysis from TNT. The Symmetric resampling values are indicated above the branches. Clade A consists of *Sauropus* and Clade C consists of *Breynia*. Thick lines indicate the subgenera and sections of *Breynia sensu lato*. The abbreviations show the previously recognised sections: CRY = *S.* sect. *Cryptogynium*, GLO = *S.* sect. *Glochidioidei*, HEM = *S.* sect. *Hemisauropus*, SAU = *S.* sect. *Sauropus*, SCH = *S.* sect. *Schizanthi*, and UNP = unplaced species.

Discussion

Phylogenetic importance of the various types of characters

The analyses of various molecular data sets (Pruesapan et al., 2008; Chapters 2 and 3), and the present analyses of the molecular data in combination with the qualitative morphological characters all produced the same three major clades in *Breynia* s.l. (Fig. 4.1). Adding the quantitative morphological characters did not change Clades A and C (Figs. 4.1--2). Only Clade B differs, being monophyletic in the analysis of the combined molecular and qualitative morphological dataset (Fig. 4.1), and paraphyletic in the total evidence analysis including quantitative morphological characters (Fig. 4.2). In the analysis of *Mallotus* by Sierra et al. (2010), the morphological data added resolution, but not support. In our study, however, the quantitative morphological characters provided a different result than the molecular evidence for Clade B, though without high support.

We prefer to use the results of the first analysis (Fig. 4.1) for the infrageneric classification of *Breynia* s.l. for three reasons: the delimitation of the character states in the quantitative morphological characters is formulaic; these characters cause an extremely high amount of homoplasy; and the resulting clades (Fig. 4.2) are less well supported than those in Fig. 4.1. One might argue that characters, which do not support clades due to a high level of homoplasy, should be pruned from the analysis. We do not wish to make these decisions a-priori, nor do we like to prune the characters after initial analyses and redo the analyses without the characters. We like to present all results as all characters will have had their share (undoubtedly in different degrees) in the evolution of a group.

Delimitation of genera

The morphological characters reinforce the conclusions drawn from earlier analyses (Kathriarachchi et al., 2006; Pruesapan et al., 2008; Chapters 2 and 3). *Breynia*, *Glochidion*, *Sauropus*, *Synostemon* could be included in a monophyletic super-*Phyllanthus* (Samuel et al., 2005; Hoffmann et al., 2006; Kathriarachchi et al., 2006). However, one 'giant' genus will make *Phyllanthus* unwieldy and unrecognizable, and it will only transfer the problem of recognizing groups to the infrageneric. Therefore, we see value in limiting the definition of *Phyllanthus*, and not including various monophyletic groups, which on the basis of our

findings are usefully recognized as distinct genera; some are in current use, thus minimising name changes.

The paraphyly of *Sauropus* can be solved in three ways: 1) *Sauropus* and *Breynia* could be united under *Breynia*, or 2) only Clade B (Fig. 4.1) with two sections of *Sauropus* and *Breynia* may be united as *Breynia*, or 3) Clade A, B and C all receive generic recognition. The last option will leave *Breynia* as it is, but will split *Sauropus* into two groups that are difficult to recognize (see below) because of the similarities in flower and fruit structure. The second option shows the same problem, the part of *Sauropus* united with *Breynia* cannot easily be distinguished from *Sauropus* Clade A. We prefer the first option for three reasons. 1) The groupings within Clades B and C have low bootstrap support (Fig. 4.1) even though BI is high. 2) The molecular reconstructions of only non-coding chloroplast data showed species of Clades A and B as a polytomy with the *Breynia* s.s. clade (Chapter 3, Fig. 3.1). 3) The union of *Sauropus* and *Breynia* will increase the recognisability of *Breynia* s.l. of their morphological similarity flower, fruit, and seed characters, which distinguishing them from *Synostemon*. Unambiguous synapomorphies for the broader concept of *Breynia* are the presence of calyx scales (absent in most *Synostemon*, but within *Breynia* s.l. a reversal in the former *Sauropus* sect. *Hemisauropus*) and the shape of the fruits, which are wider than high, and the seeds, which are smooth. *Synostemon* has fruits that are higher than wide and the seeds are prominently sculptured. The pistillate flowers also show a difference, *Breynia* has subglobose ovaries, often flattened apically, and the stigmas are split from halfway to completely, whereas *Synostemon* has ovate ovaries with an obtuse or lobed apex; the stigmas are generally not split or slightly bifid to mostly split less than halfway.

Comparing phylogeny classification with traditional classification

Some sections of *Sauropus* sensu Müller Argoviensis (1863, 1866) and Airy Shaw (1969) are corroborated by our phylogeny reconstruction. Species of *Sauropus* sections *Glochidoidei*, *Schizanthi*, and *Sauropus* form Clade A (Figs. 4.1--2). Added to this group are several unplaced species and the misplaced *S. spatulifolius* Beille, which was originally classified in section *Cryptogynium* (Figs. 4.1--4.2, Table 4.2). None of these sections are present as a monophyletic clades, and the cladograms (Figs. 4.1--2) show no supported groups within the clade. Thus, we unite all species and sections in Clade A as *Breynia* subgenus *Sauropus*. This

group contains the type of *Sauropus* (*S. albicans* Blume = *S. androgynus*). The type specimens of the three sections were not included in the analyses, but representative specimens, agreeing in morphology, were added.

Clade B (Fig. 4.1) comprises *Sauropus* sect. *Cryptogynium* (except *S. spatulifolius*) and *S.* sect. *Hemisauropus*. Both sections have to be combined, because the latter is nested within the former. The type specimens nor representatives of the species (*S. rigidius* Thwaites for section *Cryptogynium* and *S. rostatus* Miq. for sect. *Hemisauropus*) were represented in the molecular analyses, but morphologically comparable species were included. Section *Hemisauropus* is underrepresented in the sampling, because we were unable to extract DNA from the thick leaves in this group, which was probably due to an abundance of secondary metabolites. *Sauropus kerrii* Airy Shaw is probably representative for this group, which is morphologically very typical with its deviating staminate flower type [different calyx with three lobes infolded, and large, diagonally upward pointing anthers, see Van Welzen (2003): fig. 2d]. *Sauropus granulatus* Airy Shaw, with similar staminate characters as *S.* sect. *Hemisauropus*, is separate in the molecular phylogeny. Our results corroborate relationships based on pollen were *S. granulatus* groups with the main pollen type of *Sauropus* with perforate to reticulate ornamentation with subprolate to oblate spheroidal, while *S. kerrii* possesses typical *S.* sect. *Hemisauropus* pollen with a distinct perforate ornamentation, and prolate spheroidal to subprolate shape. This means that perhaps the *S.* sect. *Hemisauropus* group (*S. granulatus* excepted) may be a monophyletic group within Clade B. However, recognition of this group will make the remainder of Clade B paraphyletic. These taxa are united into one taxon under sect. *Cryptogynium* (see Müller, 1863) and, we predict it will remain a monophyletic group even when more taxa of former section *Hemisauropus* are analysed.

Clade C (Figs. 4.1--2) contains only species of *Breynia*, which we here recognize as *Breynia* sect. *Breynia*. Unfortunately, we could not include the type specimen nor the type species of *Breynia* in this molecular analysis, but other species also typical for *Breynia* (e.g. *B. retusa*) are included. However, the type species of *Breynia* (*B. disticha* J.R.Forst. & G.Forst.) was included in our previous study (Pruesapan et al., 2008; see also Figs. 2.1—3 in Chapter 2) and the results confirmed its position within *Breynia* group.

Table 4.2. Traditional classification of *Sauropus* s.s. compared with the results of the phylogenetic analysis. Names in straight characters are not present in the other column; in bold *Sauropus spatulifolius*, which is present in very different positions.

Airy Shaw (1969)	Present study
<p>Sect. <i>Glochidioidei</i> <i>S. amabilis</i>, <i>S. villosus</i></p> <p>Sect. <i>Sauropus</i> <i>S. androgynus</i>, <i>S. bonii</i>, <i>S. garrettii</i>, <i>S. repandus</i>, <i>S.rhamnoides</i>, <i>S. stipitatus</i> (= <i>S. androgynus</i>), <i>S.</i> <i>suberosus</i>, <i>S. yunnanensis</i></p> <p>Sect. <i>Schizanthi</i> <i>S. assimilis</i>, <i>S. macranthus</i>, <i>S. micrasterias</i>, <i>S.</i> <i>racemosus</i>, <i>S. thorelii</i>, <i>S. trinervius</i></p>	<p>Clade A <i>S. villosus</i></p> <p><i>S. androgynus</i>, <i>S. bonii</i>, <i>S. discocalyx</i>, <i>S. garrettii</i>, <i>S.</i> <i>poomae</i>, <i>S.rhamnoides</i>, <i>S. spatulifolius</i>, <i>S. suberosus</i>, <i>S. thyrsoiflorus</i></p> <p><i>S. assimilis</i>, <i>S. macranthus</i>, <i>S. micrasterias</i>, <i>S.</i> <i>thorelii</i>, <i>S. trinervius</i>,</p>
<p>Sect. <i>Cryptogynium</i> <i>S. amoebiflorus</i>, <i>S. asteranthos</i>, <i>S. bicolor</i>, <i>S.</i> <i>brevipes</i>, <i>S. concinnus</i>, <i>S. harmandi</i>, <i>S.</i> <i>heteroblastus</i>, <i>S. hirsutus</i>, <i>S. orbicularis</i>, <i>S. poilanei</i>, <i>S. quadrangularis</i>, <i>S. similis</i>, <i>S. spatulifolius</i></p> <p>Sect. <i>Hemisauropus</i> <i>S. granulatus</i>, <i>S. kerrii</i>, <i>S. pierrei</i>, <i>S. pulchellus</i>, <i>S.</i> <i>rostratus</i></p>	<p>Clade B <i>S. amoebiflorus</i>, <i>S. asteranthos</i>, <i>S. bicolor</i>, <i>S.</i> <i>brevipes</i>, <i>S. hirsutus</i>, <i>S. orbicularis</i>, <i>S.</i> <i>quadrangularis</i>, <i>S. similis</i></p> <p><i>S. granulatus</i>, <i>S. kerrii</i></p>

Morphological recognition of new groups (Figs. 4.3--5)

We mapped morphological character states onto one of the most-parsimonious trees obtained from the MP analysis of the combined molecular and qualitative morphological analysis (Figs. 4.3--4) to explore the taxonomic usefulness of morphological characters. The characters useful for the recognition of *Breynia* s.l. and infrageneric groups are discussed here.

Pax & Hoffmann (1922) grouped all species with large leaves, longer than 4 cm, into *S. sect. Sauropus* and *S. sect. Schizanthi*. *Sauropus sect. Glochidioidei*, proposed by Airy Shaw (1969), also shares this character. Larger leaf size is a synapomorphy for Clade A (Fig. 4.3a). Leaves shorter than 4 cm are characteristic of Clade B (*Sauropus sect. Cryptogynium* and *S. sect. Hemisauropus*) and Clade C (*Breynia*). *Synostemon*, the sister clade of *Breynia*, has small leaves as well (Fig. 4.3a) indicating that this state is plesiomorphic in *Sauropus*.

Sauropus spatulifolius has always been classified in *S.* sect. *Cryptogynium* (e.g. Airy Shaw 1969; Table 4.2), but in our molecular analysis it is part of Clade A (Pruesapan et al., 2008; Chapters 2 and 3). Its placement in this clade is corroborated by its possession of larger leaves (Fig. 4.3a), indicating the taxonomic utility of this character in the study group.

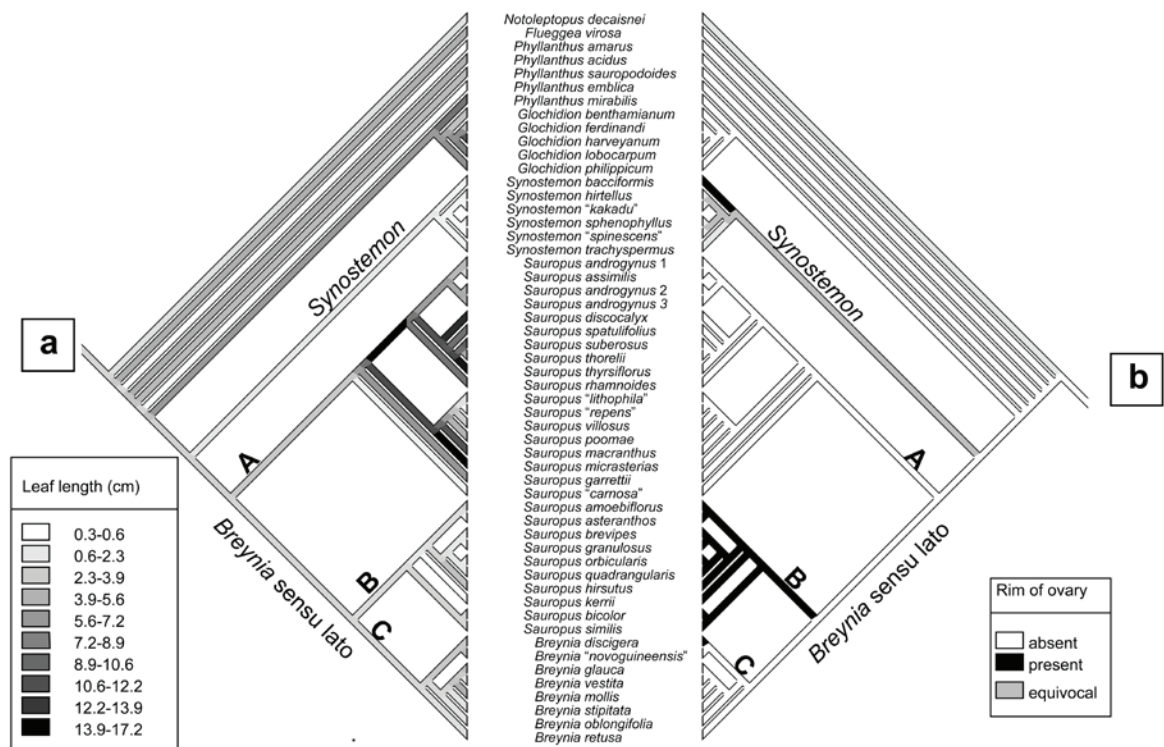


Fig. 4.3. Character state transformations in a. leaf size and b. presence of a rim at the edge of the ovary. Clade A and B are species of *Sauropus* and Clade C species of *Breynia*.

There is, however, overlap in leaf sizes between the larger-leaved (1--26 cm) and smaller-leaved (0.5--8 cm) groups (Van Welzen, 2003), accounted for by reversals and parallel developments in both groups. However, the homoplasy is due to 'exceptional' species, not continuous ranges within species. For example, in *S.* sect. *Hemisauropus* (placed by molecular evidence in the small-leaved Clade B, see above) there are a few species, not sampled here, i.e., *S. rostratus* Miq., *S. shawii* Welzen, and *S. subterblancus* (C.E.C.Fisch.) Welzen, have leaves up to 7, 11.2 and 7.5 cm long respectively. Three new species (Van Welzen & Pruesapan, in press), *S. "carnosa"* sp. nov., *S. "lithophila"* sp. nov., and *S. "repens"*

sp. nov. have small leaves, up to 1.1, 1.5, and 0.6 cm long respectively, but the molecular data show them to be part of the large-leaved Clade A .

Members of the 'larger-leaved' Clade A often have compound inflorescences (even up to 60 cm long!) rather than simple axillary fascicles, which are always found in the small-leaved Clade B (including the larger leaved species of section *Hemisauropus*) and Clade C (*Breynia* s.s.). However, Van Welzen (2003) already shows that these compound inflorescences are by not present in all species and they differ considerably in morphology (e.g., short cymes to long thyrses, latter with pistillate flowers either basal per node or apical), which is far more indicative for autapomorphies than synapomorphies. Thus, as character the non fasciculate inflorescences cannot serve as a typical character for Clade A.

In general, especially in *Sauropus*., the top of the ovary is flat, but the margin can show an upright rim or not (Figs. 4.3b, 4.5a-b). Clade A, the *Glochidioidei-Sauropus-Schizanthi* clade (Figs. 4.3b, 4.5a), has ovaries without a rim, and again, the placement of *S. spatulifolius* in this clade agrees well, because this species also lacks an ovary rim (Fig. 4.5a). The species in Clade B, the *Cryptogynium-Hemisauropus* clade (Fig. 4.3b), have ovaries with a lateral rim (Fig. 4.5b), at least between the stigmas. Within *Breynia* s.s. (Clade C, Figs. 4.1--2) the situation is somewhat more complex, with most species without a rim and only few developing it, but here the ovary never has a flat top. The ovary rim did not receive any attention by authors after Airy Shaw (1969). Instead, these authors paid special attention to the stigma position. Van Welzen (2003) reported that most species of *Sauropus* have horizontal stigmas (Figs. 4.4, 4.5a-b), while erect stigmas evolved in *S. quadrangularis* (Willd.) Müll.Arg. [Van Welzen (2003): fig. 3c], a member of section *Cryptogynium*, the species of section *Hemisauropus* [Van Welzen (2003): fig. 3d], and most species of *Breynia* (except *B. retusa* (Dennst.) Alston).

The shape of the staminate calyx is discoid with almost free to completely fused sepals in *Sauropus* (Figs. 4.4, 4.5c-d) and turbinate with fused sepals in *Breynia* (Fig. 4.4, 4.5f). However, *Sauropus granulosus* and the *Hemisauropus* group (represented by *S. kerrii*) have free sepals of which the apices are generally infolded, certainly of three of the sepals, whereby the apical part becomes connate with the basal part of the sepal.

The staminate sepal scales (Fig. 4.5c-d) are probably reduced disc glands, not secreting nectar but sealing off the staminate flower till the pollen is released (Van Welzen, 2003). The

scales are typical for *Sauropus* (Fig. 4.4), *Breynia* and few species of *Synostemon*. The scales are an apomorphy for *Breynia*--*Sauropus* (the scales show a parallel development in some *Synostemon* species). The scales are lost two times in Clade B (Fig. 4.4), in section *Hemisauropus* (*S. kerrii*) and *S. granulosus*. Pax & Hoffmann (1922) used the presence/absence of the scales to propose two subgenera: (*Eu*)*Sauropus* and *Hemisauropus*, but the results from our study disagree with their classification as only the *Hemisauropus* group is distinct.

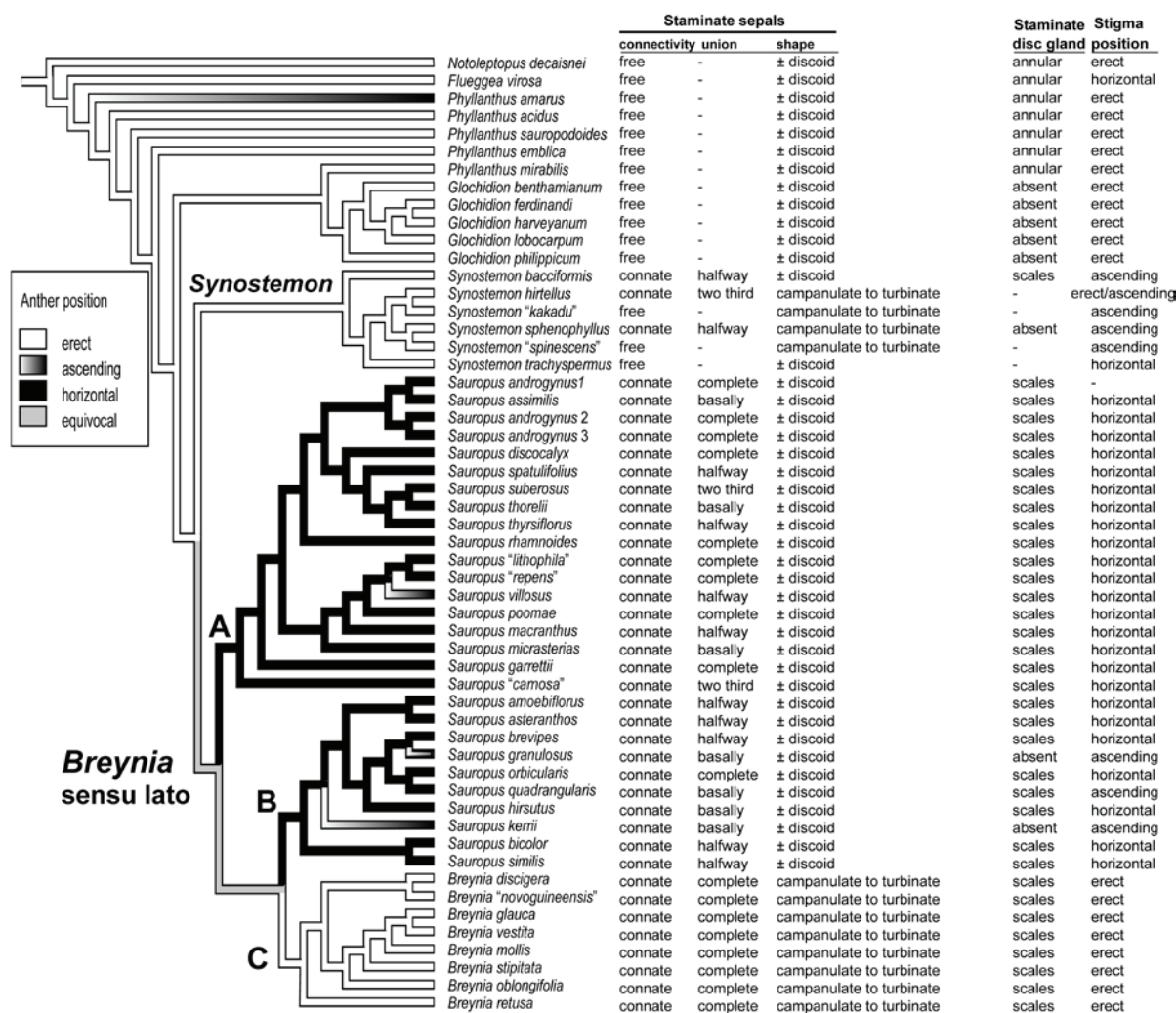


Fig. 4.4. Character state transitions in the anther position, connation and shape of the staminate sepals, the presence of a disc in the staminate flowers, and the stigma position, “-” = .not applicable. Clade A and B are species of *Sauropus* and Clade C species of *Breynia*.

The androecium shows three types (Figs. 4.4, 4.5c-f). In most *Sauropus* species, the androphore splits apically into three horizontal arms with the anthers hanging underneath (these arms may become more erect when pollen is shed; Fig. 4.5c-d). In *S. kerrii* and *S. granulatus* the anthers are much larger and semi-erect like in *S. villosus* (Fig. 4.5e). *Breynia* has a completely different type; the androecium forms a rod with the anthers vertically and longitudinally along the upper part (Fig. 4.5f).

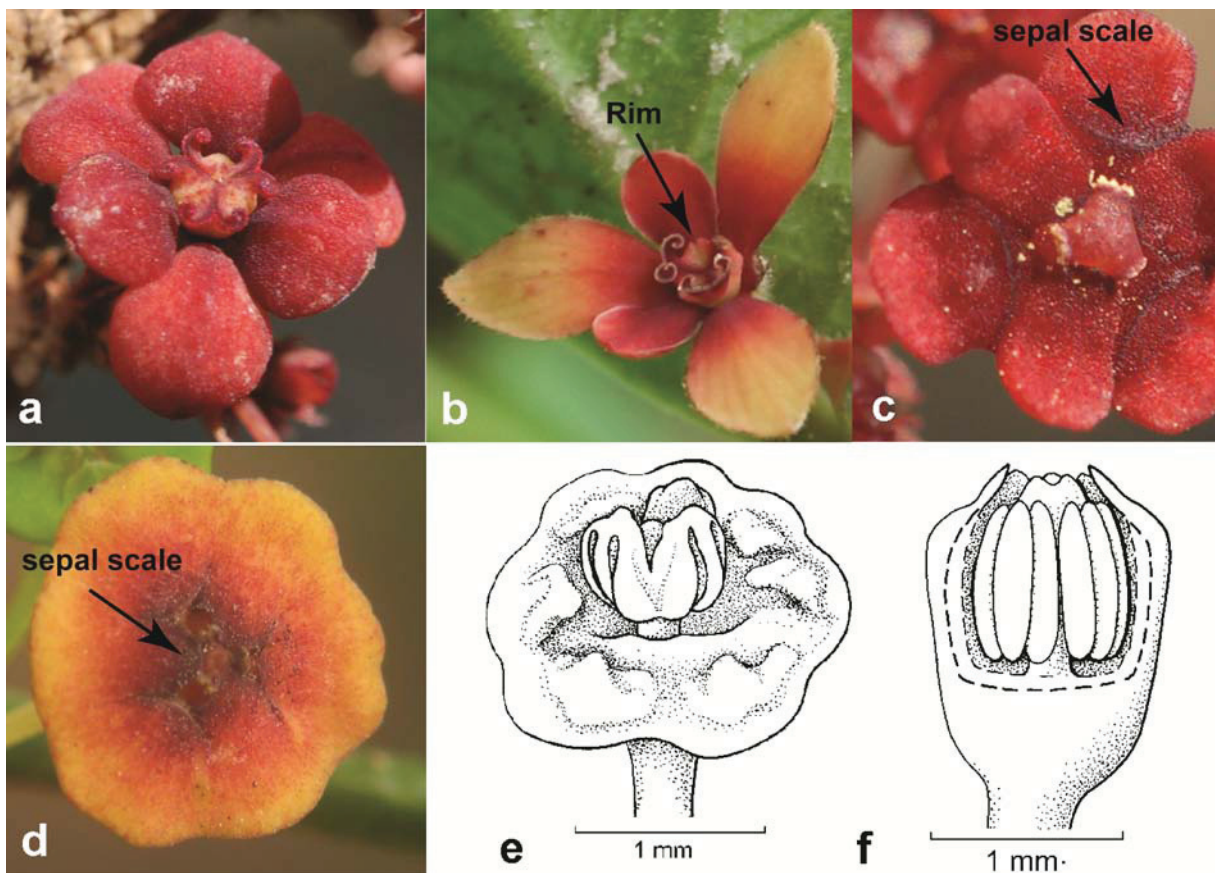


Fig. 4.5. a, b: Pistillate flowers with horizontal stigmas and absence (a) or presence (b) of a rim at the edge of the ovary. c—f: Staminate flowers with (c, d) horizontal anthers and sepals scales, but with a dissected (c) or hardly lobed calyx (d) and ascending anthers (e) or vertical anthers. a & c: *S. spatulifolius* Beille; b: *S. hirsutus* Beille; d: *S. androgynus* (L.) Merr.; e: *S. villosus* (Blanco) Merr. (*Kerr* 12619, L); f: *B. stipitata* Müll.Arg. (*Hyland* B14262, L).

The degree of connation of the staminate sepals is extremely variable (Fig. 4.4), but was used by Pax & Hoffmann (1922) to distinguish some sections in *Sauropus*. The species with (almost) completely connate sepals (Fig. 4.5d) were mainly placed in subgenus

(*Holo*)*Sauropus* by Pax & Hoffmann. Two of these species, *S. androgynus* and *S. rhamnoides*, have an almost similar widespread distribution (Van Welzen, 2003), ranging from India to East Malesia, and are difficult to distinguish (apex of leaves different). However, the phylogeny shows that they are not closely related (Figs. 4.1--2). Most species with completely connate sepals appear in Clade A (Fig. 4.4), but not as a distinct clade, thus section *Sauropus* cannot be maintained. Moreover, the same condition of connate sepals also independently appeared once in Clade B (*S. orbicularis*). Pax & Hoffmann (1922) placed the species with almost free sepals (basally connate) in section *Schizanthi* [Van Welzen (2003): fig. 2b]. However, the three species representing this section in the cladogram (Fig. 4.4, *S. assimilis*, *S. micrasterias* and *S. thorelii*), originated independently and for this reason this section cannot be maintained either. Moreover, (nearly) free sepals are also present in *Hemisauropus* as well as in *Cryptogynium* just as groups outside *Breynia-Sauropus*, e.g., *Glochidion*, most *Phyllanthus* species, and a large part of *Synostemon*. Seemingly, the basally connate sepals in *Sauropus* show at least seven reversals, which might even be a regression to an ancestral state.

Sauropus androgynus complex

Sauropus assimilis Thwaites, and three samples of *S. androgynus* form a strongly supported clade (Figs. 4.1--2), consistent with our findings based on our *matK* phylogeny (Pruesapan et al., 2008; Chapter 2). Originally, these species were placed in *S. sect. (Eu)Sauropus* (Müller Argoviensis 1863, 1866; Hooker 1887). Later *S. assimilis* was placed into *S. sect. Schizanthi* (Pax & Hoffmann 1922; Table 4.2) based on having almost free staminate sepals. The specimen of *S. assimilis* sequenced is sister to a specimen of *S. androgynus* (*Kathriarachchi*, Hoffmann & Galster 40) which was originally identified as *S. retroversus* Wight of *S. sect. Retroversi* (Pax & Hoffmann, 1922, 1931; Beille, 1927) based on the reflexed, connate staminate sepals.

Sauropus androgynus (L.) Merr. is widely cultivated from India to Australia, which may explain why it is morphologically variable. Typical are the ovate leaves with gradually tapering apices and the staminate calyx (Fig. 4.5d), which is generally completely connate and rather round and varies between 2.5--20 mm diam. The very large calyx varies from flat (typical *S. androgynus*) to recurved (former *S. retroversus*). The recurved form is thought to

be typical for Sri Lanka, but flat and recurved calices are also commonly found in Thailand. A third form in the complex is *S. assimilis*, which typically has free staminate sepal lobes. Free staminate sepal lobes are incidentally found throughout the range of *S. androgynus*. All three forms have the *S. androgynus* type of leaf.

Van Welzen (2003) placed *S. retroversus* in synonymy under *S. androgynus*. Analyses of nuclear (Chapter 3) and chloroplast (Pruesapan et al., 2008) data found former *S. retroversus* and *S. assimilis* Thwaites to be sister, and both in turn sister to typical *S. androgynus*. By contrast Kathriarachchi et al. (2006) found no support for a close relationship between former *S. retroversus* and *S. androgynus* (and thus argued that former *S. retroversus* is not a synonym of *S. androgynus*; e.g. the specimen they used as *S. androgynus* Chase 14464 (K), appeared to be *S. garrettii* Craib (see Pruesapan et al., 2008)). Yet morphologically and from our molecular studies, it is very difficult to separate the three forms, as explained above, and no sharp distinction can be made between *S. androgynus* and *S. retroversus*. The two herbarium specimens available from Sri Lanka of *Sauropus assimilis* appear to be an exceptional form of *S. androgynus*, with a deeply divided calyx, and it should be also considered as conspecific with *S. androgynus*. Based on our extensive study of herbarium material, together with morphological and molecular analysis, we place *S. assimilis* and *S. retroversus* in synonymy under *S. androgynus*.

Conclusions

Our study provides evidence for the union of *Sauropus* with *Breynia* under the latter, older name. The new circumscription of *Breynia* is monophyletic and morphologically typical are the fruits, seeds, and flowers. Our molecular and morphological phylogeny recovers three groups (Figs. 4.1--2) which we recognize as taxa within *Breynia*. We recognise Clade A as *B.* subgen. *Sauropus*, and Clades B and C as *B.* subgen. *Breynia*. Clade B and Clade C can be recognized as sections *Cryptogynium* and *Breynia* within *B.* subgen. *Breynia*. All groups have their typical characters.

This classification is formalised below.

Taxonomy

This part only comprises the taxa that are accepted by Van Welzen (2003) for Thailand and Malesia and the taxa recognized outside this area. Synonymous names are not repeated here, but can be found in Van Welzen (2003).

Breynia subgen. *Breynia*

For synonyms see under the sections below.

Breynia sect. *Breynia*

Breynia J.R.Forst. & G.Forst., Char. Gen. Pl., ed. 1: 73. 1775, nom. cons. (non *Breynia* L., Sp.

Pl.: 503. 1753, nom. rej., Capparaceae). --- Type: *Breynia disticha* J.R.Forst. & G.Forst.

= *Melanthesa* Blume, Bijdr.: 590. 1826. --- Lectotype (Webster, 1994: 46): *Melanthesa racemosa* Blume [= *Breynia racemosa* (Blume) Müll.Arg.].

= *Melanthesopsis* Müll.Arg., Linnaea 32: 74. 1863, in DC., Prodr. 15, 2: 436. 1866 ---

Lectotype (Wheeler, 1975: 537): *Melanthesopsis lucens* (Poir.) Müll.Arg. [= *Breynia fruticosa* (L.) Hook.f.].

= *Breynia* sect. *Breyniastrum* Baill., Adansonia 6: 344. 1866 --- Lectotype (selected here by Esser): *Breynia stipitata* Müll.Arg.

All species of *Breynia* s.s. (*Breynia* in the old sense) belong in the type section. These need no new combinations, and the Malesian species are still under revision by Esser & Stuppy.

Breynia* sect. *Cryptogynium* (Müll.Arg.) Welzen & Pruesapan, comb. nov. ≡ *Sauropus

Blume sect. *Cryptogynium* Müll.Arg., *Linnaea* 32: 73. 1863, in DC., *Prodr.* 15, 2: 243.

1866, as ‘*Ceratogynum*’, Hook.f., *Fl. Br. India* 5: 334. 1887, as ‘*Ceratogynum*’, Pax &

K.Hoffm. in Engl., *Pflanzenr.* IV.147.xv: 222. 1922, as ‘*Ceratogynum*’; Airy Shaw, *Kew*

Bull. 23: 43. 1969 --- Type: *Sauropus rigidus* Thwaites [= *Breynia quadrangularis*

(Willd.) Welzen & Pruesapan] (Referred originally to Wight’s genus name *Cryptogynum*,

but as the oldest available name in its rank is – erroneously – *Cryptogynium*, it must be

maintained; Airy Shaw, 1969).

= *Ceratogynum* Wight, *Icon. Pl. Ind. Orient.* 5: 26. 1852 --- Type: *Ceratogynum rhamnoides*

Wight [= *Breynia quadrangularis* (Willd.) Welzen & Pruesapan].

= *Sauropus* Blume sect. *Hemisauropus* Müll.Arg. in DC., *Prodr.* 15, 2: 243. 1966; Airy Shaw,

Kew Bull. 23: 55. 1969 ≡ *Sauropus* Blume subgen. *Hemisauropus* (Müll.Arg.) Pax &

K.Hoffm. in Engl., *Pflanzenr.* IV.147.xv: 225. 1922 --- Type: *Sauropus rostratus* Miq. [=

Breynia miqueliana Welzen & Pruesapan].

= *Breyniopsis* Beille, *Bull. Soc. Bot. France* 72: 157. 1925, in M.H.Lecomte, *Fl. Indo-Chine*

5: 630. 1927 --- Type: *Breyniopsis pierrei* Beille [= *Breynia pierrei* (Beille) Welzen &

Pruesapan].

Breynia amoebiflora* (Airy Shaw) Welzen & Pruesapan, comb. nov. ≡ *Sauropus

amoebiflorus Airy Shaw, *Kew Bull.* 23: 45. 1969 --- Type: Thailand (Siam),

Southwestern, Ratchaburi Prov.: Ratchaburi (Ratburi), *Kerr 9023* (holotype: K!; isotypes:

BM!, L!, P!).

Breynia asteranthos (Airy Shaw) Welzen & Pruesapan, comb. nov. \equiv *Sauropus asteranthos*

Airy Shaw, Kew Bull. 23: 47. 1969 --- Type: Thailand (Siam), Northeastern (Udon Thani Circle), Nakhom Phanom Prov.: Dawn Tan, *Kerr 21530* (holotype: K!; isotypes: BM!, L!, P!).

Breynia bicolor (Craib) Welzen & Pruesapan, comb. nov. \equiv *Sauropus bicolor* Craib, Bull.

Misc. Inform. Kew: 11. 1914 = *Sauropus rigidus* Craib, Bull. Misc. Inform.: 457. 1911, nom. inval., non Thwaites (1864) --- Lectotype (Van Welzen, 2003: 347): Thailand (Siam), Northern, Chiang Mai Prov.: Doi Sutep, *Kerr 651* (holotype: K!; isotypes: BM!, K!).

Note: For more synonyms see Van Welzen (2003).

Breynia brevipes (Müll.Arg.) Welzen & Pruesapan, comb. nov. \equiv *Sauropus brevipes*

Müll.Arg., Linnaea 32: 73. 1863 = *Aalius brevipes* (Müll.Arg.) Kuntze, Rev. Gen. Pl. 2: 591. 1891 --- Type: India, Prome, *Wallich 23?* (holotype: G-DC, 2 sheets, IDC microfiche DC herbarium 2461/12, 13!).

Note: For more synonyms see Van Welzen (2003).

Breynia delavayi (Croizat) Welzen & Pruesapan, comb. nov. \equiv *Sauropus delavayi* Croizat, J.

Arnold Arbor. 21: 496. 1940 --- Type: China, Yunnan, *Delavay 2845* (holotype: A!; isotypes: A!, P).

Breynia granulosa (Airy Shaw) Welzen & Pruesapan, comb. nov. \equiv *Sauropus granulosa*

Airy Shaw, Kew Bull. 23: 53. 1969 --- Type: Thailand (Siam), North-eastern (Udawn Circle), Sakon Nakhon Prov.: Wa Nawn, *Kerr 8500* (holotype: K!; isotype: BM!).

Breynia harmandii (Beille) Welzen & Pruesapan, comb. nov. \equiv *Sauropus harmandii* Beille

in Lecomte, Fl. Indo-Chine 5: 657. 1927 --- Type: Cambodia (Cambodge): *Harmand s.n.* (holotype: P!).

Breynia heteroblasta (Airy Shaw) Welzen & Pruesapan, comb. nov. \equiv *Sauropus*

heteroblastus Airy Shaw, Kew Bull. 23: 48. 1969 --- Type: S Vietnam: Dalat and vicinity, *Squires 921* (holotype: K!; isotypes: A!, M!, P!).

Breynia hirsuta (Beille) Welzen & Pruesapan, comb. nov. \equiv *Sauropus hirsutus* Beille in

Lecomte, Fl. Indo-Chine 5: 657. 1927 --- Lectotype (Welzen, 2003: 356): Cambodia: Samrong-tong, *Pierre 564* (holotype: P).

Breynia kerrii (Airy Shaw) Welzen & Pruesapan, comb. nov. \equiv *Sauropus kerrii* Airy Shaw,

Kew Bull. 23: 52. 1969. --- Type: Thailand (Siam), Eastern (Ubon Circle), Ubon Ratchathani Prov.: Chiet, *Kerr 21541* (holotype: K!; isotypes: BM!, L!, P!).

Breynia miqueliana Welzen & Pruesapan, nom. nov. \equiv *Sauropus rostratus* Miq., Eerste

Bijv.: 179, 447. 1861 \equiv *Aalius rostratus* (Miq.) Kuntze, Rev. Gen. Pl. 2: 591. 1891, as 'rostrata' --- Lectotype (Welzen, 2003: 370): Indonesia, Sumatra, Palembang Prov.: River Lamatang near Koeripan (Kuripan), *Teysmann HB 3678* (holo U).

Notes: The combination *Breynia rostrata* is already in use. The epithet honours the prolific Dutch botanical author Friedrich Anton Wilhelm Miquel (1811-1871) (see http://en.wikipedia.org/wiki/Friedrich_Anton_Wilhelm_Miquel). For a heterotypic synonym see Van Welzen (2003).

Breynia orbicularis (Craib) Welzen & Pruesapan, comb. nov. \equiv *Sauropus orbicularis* Craib, Bull. Misc. Inform. Kew: 284. 1914--- Type: Thailand, Chiang Mai Prov.: Doi Sutep, *Kerr 2635* (holotype: K!; isotypes: A!, BM!, CAL!).

Note: For heterotypic synonyms see Van Welzen (2003).

Breynia pierrei (Beille) Welzen & Pruesapan, comb. nov. \equiv *Breyniopsis pierrei* Beille, Bull. Soc. Bot. France 72: 158. 1925 \equiv *Sauropus pierrei* (Beille) Croizat, J. Arnold Arbor. 21: 494. 1940 --- Syntypes: Vietnam, Cochinchine, Prov. Bien-Hoa: Trang-bon, *Evrard 110* (P!); Vietnam: Bao Chang, *Pierre 1792* (A!, P!); Vietnam, Prov. Bien-Hao: Gia-ray, *Poilane 2442* (P!).

Breynia poilanei (Beille) Welzen & Pruesapan, comb. nov. \equiv *Sauropus poilanei* Beille in Lecomte, Fl. Indo-Chine 5: 653. 1927 --- Type: Vietnam, Annam, prov. Phanrang: Ca-na, *Poilane 5950* (holotype: P!; isotypes: A!, P!).

Breynia po-khantii (Chakrab. & M.Gangop.) Welzen & Pruesapan, comb. nov. \equiv *Sauropus po-khantii* Chakrab. & M.Gangop., J. Econ. Taxon. Bot. 20: 531, Fig. 7. 1996 --- Type: Myanmar (Burma), Tenasserim, Mergui dist.: Chaegleya, *Maung Po Khant 13451* (holotype: CAL)

Note: The drawing in Fig. 7 shows the plant with small leaves, therefore, the species is placed in this section. However, the rim along the margin of the ovary makes the placement uncertain.

Breynia pulchella (Airy Shaw) Welzen & Pruesapan, comb. nov. \equiv *Sauropus pulchellus* Airy Shaw, Kew Bull. 23: 54. 1969 --- Thailand (Siam), Eastern Rachasima Circle, Nakhon Ratchasima Prov. (Korat): Ta Chang, *Kerr 20472* (holotype: K!; isotype: BM!).

Breynia quadrangularis (Willd.) Welzen & Pruesapan, comb. nov. \equiv *Phyllanthus quadrangularis* Willd., Sp. Pl. 4: 585. 1805 \equiv *Sauropus quadrangularis* (Willd.) Müll.Arg., Linnaea 32: 73. 1863 \equiv *Aalius quadrangularis* (Willd.) Kuntze, Rev. Gen. Pl. 2: 591. 1891 --- Type: India: *Hb. Willdenow 17985* (holotype: B-W; IDC microfiche 7440!).

Note: For heterotypic synonyms see Van Welzen (2003).

Breynia shawii (Welzen) Welzen & Pruesapan, comb. nov. \equiv *Sauropus shawii* Welzen, Blumea 48: 372, map 4. 2003 --- Type: Malaysia, Sabah, Lahad Datu: Ulu Sungei Segamat, *P.F. Stevens et al. 513* (holotype: L!; isotypes: A!, KEP!).

Breynia similis (Craib) Welzen & Pruesapan, comb. nov. \equiv *Sauropus similis* Craib, Bull. Misc. Inform. Kew: 57. 1911 --- Lectotype (Van Welzen, 2003: 372): Thailand, Chiang Mai: Doi Sutep, *Kerr 1788* (holotype: K!; isotype: BM!).

Breynia subterblanca (C.E.C.Fisch.) C.E.C.Fisch., Bull. Misc. Inform. Kew: 98. 1939, as
'*subterblancum*' ≡ *Glochidion subterblancum* C.E.C.Fisch., Bull. Misc. Inform. Kew:
211. 1927 ≡ *Sauropus subterblancus* (C.E.C.Fisch.) Welzen, Blumea 46: 504. 2001 ---
Type: Myanmar (Burma), South Tenasserim: Kyein Chaung, C.E. Parkinson 1669
(holotype: K!; isotype: K!).

Breynia tsiangii (P.T.Li) Welzen & Pruesapan, comb. nov. ≡ *Sauropus tsiangii* P.T.Li, Acta
Phytotax. Sin. 25: 135. 1987. --- Type: China, Guangxi, Longzhou: Shuikou, *Zhi-Nan*
Exped. s.n. (Inst. Bot. Acad. Sin. Herb. 990841) (holotype: PE).

Note: Based on the protologue description of the species, it is placed in *B.* sect.

Cryptogynium.

Breynia subgen. *Sauropus* (Blume) Welzen & Pruesapan, comb. et stat. nov. ≡ *Sauropus*
Blume, Bijdr.: 595. 1826 ≡ *Sauropus* Blume sect. *Eusauropus* Müll.Arg., Linnaea 32: 72.
1863, nom. inval., Art. 22.2, in DC., Prodr. 15, 2: 240. 1866, Hook.f., Fl. Br. India 5: 332.
1887 ≡ *Sauropus* Blume subgen. *Holosauropus* Pax & K. Hoffm. in Engl., Pflanzenr.
IV.147.xv: 216. 1922, nom. inval., Art. 22.2 --- Lectotype (G.L. Webster, 1994: 81):
Sauropus albicans Blume [= *Breynia androgyna* (L.) Welzen & Pruesapan]
= *Aalius* Rumph. [Herb. Amboin.: 207. 1743, nom. inval., pre-Linnean, Lam., Encycl. Méth.
Bot. 1, 1: 1. 1783, nom. inval., Art. 32.1(d)] ex Kuntze, Rev. Gen. Pl. 2: 590. 1891, nom.
superfl. --- Lectotype (see Welzen, 2003: 331): *Aalius androgynus* (L.) Kuntze [= *Breynia*
androgyna (L.) Welzen & Pruesapan; see also Welzen, 2003, for all problems with the
interpretation of the name *Aalius*].

= *Sauropus* Blume sect. *Sphaeranthi* Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xv: 220.

1922 --- Type: *Sauropus stipitatus* Hook.f. [= *Breynia gynophora* Welzen & Pruesapan].

= *Sauropus* Blume sect. *Retroversi* Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xv: 221. 1922

--- Type: *Sauropus retroversus* Wight [= *Breynia androgyna* (L.) Welzen & Pruesapan].

= *Sauropus* Blume sect. *Schizanthi* Pax & K.Hoffm. in Engl., Pflanzenr. IV.147.xv: 221. 1922

--- Lectotype (Welzen, 2003: 331): *Sauropus trinervius* Wall. ex Müll.Arg. [= *Breynia trinervia* (Wall. ex Müll.Arg.) Welzen & Pruesapan].

= *Sauropus* Blume sect. *Glochidioidei* Airy Shaw, Kew Bull. 23: 51. 1969 --- Type: *Sauropus*

villosus (Blanco) Merr. [= *Breynia villosa* (Blanco) Welzen & Pruesapan].

Breynia amabilis (Airy Shaw) Welzen & Pruesapan, comb. nov. ≡ *Sauropus amabilis* Airy

Shaw, Kew Bull. 23: 49. 1969 --- Type: Thailand (Siam), prov. Nakhon Sawan (Nakawn Sawan): Hua Wai, *Put 4102* (holotype: K!; isotypes: A!, BK!, BM!, L!, P!).

Breynia androgyna (L.) Welzen & Pruesapan, comb. nov. ≡ *Clutia androgyna* L., Syt. Nat.

ed. 12, 2: 663. 1767, Mant. Pl. 1: 128. 1767 ≡ *Aalius androgyna* (L.) Kuntze, Revis. Gen.

Pl. 2: 591. 1891 ≡ *Sauropus androgynus* (L.) Merr., Bull. Bur. Forest. Philipp. Is. 1 (1903)

30. --- Lectotype (Van Welzen, 2003: 340): *Hb. Linnaeus 1206.14* (holotype: LINN).

= *Sauropus assimilis* Thwaites, Enum. Pl. Zeyl.: 284. 1861, syn. nov. --- Type: Sri Lanka

(Ceylon), Central Prov.: Allagalla, *Thwaites 3134* (holotype: K!).

= *Sauropus convexus* J.J.Sm., Bull. Jard. Bot. Buitenzorg ser. 3, 6: 82. 1924, syn. nov. ---

Neotype (selected here): Indonesia, Java: Bogor, *Hortus Bogoriensis* s.n., cultivated (L, barcode L 0138208). Former syntypes were based on living collections of which there are no vouchers): Indonesia, Java: Bogor, *Hortus Bogoriensis XV.J.B.IV.1* (died 1950) ajd

XV.J.B.V.5 (died 1945), originally from Leiden Botanical Garden. Smith indicates that there are minor differences in the staminate and pistillate flowers with *B. androgyna*, which fall well within the variation of this species.

Note: For more synonyms see Van Welzen (2003).

Breynia asymmetrica (Welzen) Welzen & Pruesapan, comb. nov. \equiv *Sauropus asymmetricus*

Welzen, *Blumea* 48: 344. 2003 --- Type: Indonesia, Sumatra, *Yates 1241* (holotype: BM!, barcode BM000606476; isotype: P!).

Breynia beillei Welzen & Pruesapan, nom. nov. \equiv *Sauropus racemosus* Beille in Lecomte, *Fl.*

Indo-Chine 5: 648. 1927--- Type: [Vietnam], Tonkin; vallée de Lankok, Mont Bavi, *Balansa 3202* (holotype: P!; isotype: P!).

Note: The combination *Breynia racemosa* (Blume) Müll.Arg. is already in use. The latter species has no other synonyms, therefore, a new name is created within *Breynia*.

Breynia bishnupadae (M.Gangop. & Chakrab.) Welzen & Pruesapan, comb. nov. \equiv

Sauropus bishnupadae M.Gangop. & Chakrab., *J.Econ. Taxon. Bot.* 20: 524, fig. 2A--D. 1996 --- Type: India, Sikkim: Gulma, *E.A.C. Modder 114* (holotype: CAL).

Note: This species is placed here due to its large leaves and pistillate flowers without a raised margin on top of the ovary. This information has been provided by the illustration in the protologue.

Breynia bonii (Beille) Welzen & Pruesapan, comb. nov. \equiv *Sauropus bonii* Beille in Lecomte, Fl. Indo-Chine 5: 651. 1927--- Type: [Vietnam], Tonkin: Mont Kien-khé, *Bon 2873* (holotype: P, 3 sheets!; isotype: A!).

Breynia discocalyx (Welzen) Welzen & Pruesapan, comb. nov. \equiv *Sauropus discocalyx* Welzen, Blumea 46: 501, fig. 1. 2001 --- Type: Thailand, Peninsular: Khao Saideng, near Ranong, *van Beusekom & Phengkhlai 566* (holotype: L!; isotypes: AAU!, BKF!, C!, E, K!, P!).

Breynia garrettii (Craib) Welzen & Pruesapan, comb. nov. \equiv *Sauropus garrettii* Craib, Bull. Misc. Inform. Kew: 284. 1914 --- Type: Thailand, Doi Inthanon, N by E of the Pah Ngeam, *Garrett 37* (holotype: K!; isotype: BM!, L!).

Note: For synonyms see Van Welzen (2003).

Breynia gour-maitii (Charkab. & M.Gangop.) Welzen & Pruesapan, comb. nov. \equiv *Sauropus gour-maitii* Chakrab. & M.Gangop., J.Econ. Taxon. Bot. 20: 529, Fig. 5A—E. 1996 --- Type: India, Kerala, Trivandrum dist.: way to Chamungi, *Mohanan 61883* (holotype: CAL).

Note: The drawing in Fig. 5A—E by Chakrabarty & Gangopadhyay (1996) shows that the species has quite large leaves with the staminate flower typical for species of former section *Schizanthi*, included here in subgenus *Sauropus*.

Breynia gynophora Welzen & Pruesapan, nom. nov. \equiv *Sauropus stipitatus* Hook.f., Fl. Brit. India 5: 333. 1887 --- Type: India, Sikkim: Darjeeling, *Griffith s.n.* (holotype: K!).

Note: The combination *Breynia stipitata* Müll.Arg. is already in use. The epithet *gynophora* refers to the stalked ovary and fruit of this species.

Breynia kitanovii (Thin) Welzen & Pruesapan, comb. nov. \equiv *Sauropus kitanovii* Thin, Euphorbiac. Vietnam: 49. 1996. --- Type: Vietnam, Hoa Binh: Luong Son, Lam Son. *N.V. Tiep Not-2790* (holotype: HNU.).

Note: The placement of this species may be incorrect as the leaf size and staminate flower mentioned by Thin are also reminiscent of the *Hemisauropus* group in *Breynia* subgenus *Breynia*.

Breynia lanceolata (Hook.f.) Welzen & Pruesapan, comb. nov., nom. nov. [non *B. rhamnoides* (Willd.) Müll.Arg.] \equiv *Sauropus lanceolatus* Hook.f., Fl. Brit. India 5: 333. 1887 --- Type: India, East Bengal: Mishmee, *Griffith KD 4825* (holotype: K!; '4828' on sheet; N.B. there are more sheets of *Griffith KD 4828* at K, one is a paratype of *S. macrophyllus* Hook.f.).

= *Sauropus rhamnoides* Blume, Bijdr.: 596. 1825 \equiv *Aalius rhamnoides* (Blume) Kuntze, Revis. Gen. Pl. 2: 591. 1891, as '*rhamnoides*' --- Lectotype (Welzen, 2003: 367): Indonesia, Java: Montis Salak, *Blume s.n.* (L., barcode L 0138511).

Note: *Sauropus lanceolatus* is a synonym of *Sauropus rhamnoides* Blume. However, the combination *Breynia rhamnoides* (Willd.) Müll.Arg. already exists. For more synonyms see Van Welzen (2003).

Breynia macrantha (Hassk.) Welzen & Pruesapan, comb. nov. \equiv *Sauropus macranthus*

Hassk., Retzia 1: 166. 1855. ---Type: Indonesia: Bogor, Hortus Bogoriensis, *Teysmann s.n.* (holotype: L, barcode L 0138428).

Note: For synonyms see Van Welzen (2003).

Breynia maichauensis (Thin) Welzen & Pruesapan, comb. nov. \equiv *Sauropus maichauensis*

Thin, J. Biol. (Vietnam) 14: 24. 1992 --- Type: Vietnam, Cao Bang: Trung Khanh, *P.K. Loc P 4863* (holotype: HNU).

Note: Placed in this subgenus based on the protologue description.

Breynia micrasterias (Airy Shaw) Welzen & Pruesapan, comb. nov. \equiv *Sauropus*

micrasterias Airy Shaw, Kew Bull. 14: 354. 1960. --- Type: Malaysia, Sarawak, 1st

Division: rock formation (Bau series) W. and E. of passage of Sungei Serin (30 miles S of Kuching), *Jacobs 5179* (holotype: K!; isotype: L!).

Breynia poomae (Welzen & Chayam.) Welzen & Pruesapan, comb. nov. \equiv *Sauropus poomae*

Welzen & Chayam., Kew Bull. 56: 652. 2001--- Type: Thailand, Chiang Rai Prov.: Doi Tung *Pooma, Mauric & Greijmans 1470* (holotype: BKF!).

Breynia repanda (Müll.Arg.) Welzen & Pruesapan, comb. nov. \equiv *Sauropus repandus*

Müll.Arg., Flora 55: 2. 1872 --- Type: India, prov. Sikkim: Nohore, *T. Anderson 922* (holotype: B, lost).

Breynia reticulata (S.L.Mo ex P.T.Li) Welzen & Pruesapan, comb. nov. \equiv *Sauropus*

reticulatus S.L.Mo ex P.T.Li, Acta Phytotax. Sin. 25: 133. 1987--- Type: China, Guangxi: Jingxi, Z.Y. Wei 46023 (holotype: IBG, acronym unknown, also not spelled out in protologue, n.v.).

Note: Based on the large size of the leaves as mentioned in the protologue, the species is placed in this subgenus.

Breynia saksenana (Manilal, Prasann. & Sivar.) Welzen & Pruesapan, comb. nov. \equiv

Sauropus saksenanus Manilal, Prasann. & Sivar., J. Ind. Bot. Soc. 64: 294. 1985, as 'saksenianus'. --- Type: India, Kerala: Nilikkal, Silent Valley, *Prasannaumar SV 10398* (holotype: CALI).

Breynia spatulifolia (Beille) Welzen & Pruesapan, comb. nov. \equiv *Sauropus spatulifolius*

Beille in Lecomte, Fl. Indo-Chine 5: 652. 1927, as '*spathulaefolius*' --- Type: Vietnam, Tonkin: Lang-nhoi, *Bon 9130* (holotype: P!).

Note: The epithet, though unusual, is without an "h" after the "t", and according to ICBN art. 60.1 Ex 1 and 61.1 this is not correctable (McNeill et al., 2006).

Breynia suberosa (Airy Shaw) Welzen & Pruesapan, comb. nov. \equiv *Sauropus suberosus* Airy

Shaw, Kew Bull. 23: 42. 1969 --- Type: Thailand, Peninsular, Phuket Prov.: Khao Thong Lang, NW of Nai Chong, *Hansen & Smitinand 12030* (holotype: K!; isotype: L!, SING!).

Breynia thoi (Thin) Welzen & Pruesapan, comb. nov. \equiv *Sauropus thoi* Thin, Euphorbiac.

Vietnam: 48. 1996 --- Type: Vietnam, Hoa Binh: Luong Son, Lam Son, *Thin, Loc, Binh, Thuoc, Chan NT 1990* (holotype: HNU).

Note: Based on the description the species is placed in this subgenus.

Breynia tiepii (Thin) Welzen & Pruesapan, comb. nov. \equiv *Sauropus tiepii* Thin, Euphorbiac.

Vietnam: 49. 1996--- Type: Vietnam, Coa Bang: Trung Khanh, *N.V. Tiep Not-2278* (holotype: HNU).

Note: Based on the protologue description of the species, it is placed in *Breynia* subgen.

Sauropus.

Breynia thorelii (Beille) Welzen & Pruesapan, comb. nov. \equiv *Sauropus thorelii* Beille in

Lecomte, Fl. Indo-Chine 5: 649. 1927. --- Type: Laos, Pak-lay: Lakhone, *Thorel 3227* (holotype: P!; isotype: K!).

Breynia thyrsiflora (Welzen) Welzen & Pruesapan, comb. nov. \equiv *Sauropus thyrsiflorus*

Welzen, Blumea 46: 503, fig. 2. 2001 --- Type: Thailand, (Southwestern,) Kanchanaburi, Sangklaburi Distr., Lai Wo Subdistr.: Toong Yai Naresuan Wildlife Reserve, Ban Sanah Pawng area (Karen hilltribe village), *Maxwell 94-499* (holotype: L!; isotypes: A!, CMU).

Breynia trinervia (Hook.f. & Thoms. ex Müll.Arg.) Welzen & Pruesapan, comb. nov. \equiv

Sauropus trinervius Hook.f. & Thoms. ex Müll.Arg., Linnaea 32: 72. 1863 --- Syntypes:

India: Mts. Khasia, *J.D. Hooker & T. Thomson* s.n. (G-DC?, K!); India: Botanical Garden

Calcutta, *Wallich 7922A* (G-DC?, K!, 2 sheets); India: Silhet, *Wallich 7922B* (G-DC?, K!, 2 sheets).

Breynia villosa (Blanco) Welzen & Pruesapan, comb. nov. \equiv *Kirganelia villosa* Blanco, Fl.

Filip.: 712. 1837 \equiv *Sauropus villosus* (Blanco) Merr., Contrib. Arn. Arb. 8: 86. 1934 ---

Neotype (Welzen, 2003): Philippines, Luzon, Rizal Prov.: *Merrill Species Blancoanae*

931 (holotype: L!; isotypes: A!, BM!, K!, NSW!, NY!, P!, US!).

Note: For heterotypic synonyms see Van Welzen (2003).

Breynia yanhuiana (P.T.Li) Welzen & Pruesapan, comb. nov. \equiv *Sauropus yanhuianus*

P.T.Li, Acta Phytotax. Sin. 25: 134. 1987--- Type: China, Yunnan: Cangyuan, Nanla, *Y.H.*

Li 12549 (holotype: YNTBI, acronym unknown, also not spelled out in protologue).

Note: Based on the protologue description of the species, it is placed in *Breynia* subgen.

Sauropus.

Unplaced species

One species could not be classified into subgenus or section because the descriptions were not adequate, and type specimens were not available.

Breynia varieri (Sivar. & Balach.) Welzen & Pruesapan, comb. nov. \equiv *Sauropus varieri*

Sivar. & Balach., J. Econ. Taxon. Bot. 5: 918. 1984. --- Type: India, Kerala, Malappuram

dist.: Kottakkal Arya Vaidya Sala Herbal Garden, *Indu AVS 1579* (holotype: CAL; isotypes:

CALI, MH).

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Appendix 4.1. Specimens sampled for this study.

a. Species, locality, voucher number, GenBank accession number (and citations for previously published data) for ITS, *PHYC*, *accD-psaI*, *trnS-trnS*, “---” indicates missing data. In Figs. 4.1—4, ^a indicated as *Sauropus androgynus*1, ^b indicated *Sauropus androgynus*2, and ^c indicated as *Sauropus androgynus*3.

OUTGROUP TAXA: *Notoleptopus decaisnei* (Benth.) Voronts. & Petra Hoffm., Queensland, Australia, *Fraser* 267 (L), AM745832 (Vorontsova et al., 2007), GQ503431, GQ503491, GQ503555; *Flueggea virosa* (Roxb. ex Willd.) Voigt, Thailand, *Larsen et al.* 45328 (L), GQ503362, GQ503420, GQ503481, ---.

INGROUP TAXA: *Breynia discigera* Müll.Arg., N. Sumatra, Indonesia, *Takeuchi et al.* 18873 (L), EU623550 (Pruesapan et al., 2008), GQ503410, ---, ---; *Breynia glauca* Craib, Nong Khai, Thailand, *Pooma et al.* 2702 (L), EU623551 (Pruesapan et al., 2008), GQ503411, ---, GQ503532; *Breynia mollis* J.J.Sm., Papua New Guinea, Indonesia, *Sands 1076* (L), EU623552 (Pruesapan et al., 2008), GQ503412, ---, ---; *Breynia “novoguineensis”* sp. nov. (Esser & Stuppy, unpubl.) Papua, Indonesia, *Baker et al.* 37 (L), EU623549 (Pruesapan et al., 2008), GQ503409, GQ503472, GQ503530; *Breynia oblongifolia* (Müll.Arg.) Müll.Arg., Australia, *Forster 32745* (NE), GQ503355, GQ503414, GQ503475, GQ503534; *Breynia retusa* (Dennst.) Alston, Vientiane, Laos, *Soejarto & Southavong 10783* (L), GQ503358, GQ503417, GQ503477, GQ503536; *Breynia stipitata* Müll.Arg., Australia, *Bruhl 2478* (NE), GQ503359, GQ503418, GQ503478, GQ503537; *Breynia vestita* Warb., Papua, Indonesia, *Barker & Beaman 70* (L), EU623553 (Pruesapan et al., 2008), GQ503419, GQ503480, GQ503540; *Glochidion benthamianum* Domin, Australia, *Bruhl 1026* (NE), GQ503363, ---, GQ503482, GQ503541; *Glochidion ferdinandi* (Müll.Arg.) Pax & Hoffm., Australia, *Bruhl 2457* (NE), GQ503366, GQ503421, GQ503484, GQ503543; *Glochidion harveyanum* Domin, Australia, *Bruhl 2527* (NE), GQ503368, GQ503423, GQ503486, GQ503545; *Glochidion lobocarpum* (Benth.) F.M.Bailey, Australia, *Bruhl 1146* (NE), GQ503371, GQ503424, GQ503488, GQ503548; *Glochidion philippicum* (Cav.) C.B.Rob., Australia, *Forster 29379* (NE), GQ503373, GQ503426, GQ503490, GQ503550; *Phyllanthus acidus* (L.) Skeels, Saraburi, Thailand, *Van Welzen 2003-14* (L), EU623556 (Pruesapan et al., 2008), GQ503432, GQ503492, GQ503556; *Phyllanthus amarus* Schumach. & Thonn., Chachoengsao, Thailand, *Van Welzen 2006-5* (L), EU623557 (Pruesapan et al., 2008), GQ503433, GQ503493, GQ503557; *Phyllanthus emblica* L., Saraburi, Thailand, *Van Welzen 2003-11* (L), GQ503378, GQ503434, GQ503494, GQ503558; *Phyllanthus mirabilis* Müll.Arg., Phrae, Thailand, *Sirichamorn YSM 2009-05* (L), HM132100, HM132101, HM132099, HM132102; *Phyllanthus sauropodoides* Airy Shaw, Queensland, Australia, *Forster 29857* (L), EU623558 (Pruesapan et al., 2008), GQ503436, GQ503496, GQ503560; *Sauropus amoebiflorus* Airy Shaw, Thailand, *Kerr 19655* (P), GQ503379, GQ503437, GQ503498, GQ503562; *Sauropus androgynus* (L.) Merr., Sri Lanka, ^a*Kathriarachchi et al.* 40 (K), AY936747 (Kathriarachchi et al., 2006), GQ503459, GQ503517, GQ503588; Queensland, Australia, ^b*Telford & Bruhl 13056* (L), GQ503380, GQ503438, ---, GQ503563, Chachoengsao, Thailand, ^c*Van Welzen 2006-4* (L), EU623563 (Pruesapan et al., 2008), GQ503439, GQ503500, GQ503564; *Sauropus assimilis* Thwaites, Pelawatte, Sri Lanka, *Kostermans 27871* (L), GQ503381, ---, ---, ---; *Sauropus asteranthos* Airy Shaw, Nakhon Sawan, Thailand, *Esser 99-13* (L), EU623565 (Pruesapan et al., 2008), ---, GQ503501, ---; *Sauropus bicolor* Craib, Chiang Mai, Thailand, *Esser 99-21* (L), EU623567 (Pruesapan et al., 2008), ---, GQ503503, ---; *Sauropus brevipes* Müll.Arg., Phetchaburi, Thailand, *Middleton et al.* 974 (L), EU623568 (Pruesapan et al., 2008), ---, ---, ---; *Sauropus “carnosa”* sp. nov., Surat Thani, Thailand, *Middleton et al.* 4070 (L), GQ503401, ---, ---, GQ503594; *Sauropus discocalyx* Welzen, Ranong, Thailand, *Beusekom & Phengklai 566* (L), GQ503387, ---, ---, GQ503569; *Sauropus garrettii* Craib, Guizhou, China, *Sino-American Guizhou Botanical Expedition 1872* (L), EU623570 (Pruesapan et al., 2008), GQ503444, GQ503507, GQ503572; *Sauropus granulosus* Airy Shaw, Sakon Nakhon, Thailand, *Pooma et al.* 4257 (L), GQ503390, ---, ---, ---; *Sauropus hirsutus* Beille, Thailand, *Larsen et al.* 33993 (P), GQ503391, GQ503445, ---, ---; *Sauropus kerrii* Airy Shaw, Tak, Thailand, *Van Beusekom & Phengklai 1065* (P), EU623574 (Pruesapan et al., 2008), GQ503452, ---, GQ503579; *Sauropus “lithophila”* sp. nov., Chonburi, Thailand, *Phonsena et al.* 5594 (L), ---, GQ503464, GQ503522, GQ503595; *Sauropus macranthus* Hassk., Queensland, Australia, *Telford & Bruhl 13107* (L), GQ503396, ---, ---, ---; *Sauropus micrasterias* Airy Shaw, Sarawak, Malaysia, *Erwin & Chai S 27479* (L), EU623578 (Pruesapan et al., 2008), GQ503455, ---, GQ503582; *Sauropus orbicularis* Craib, Vientiane, Laos, *Soejarto & Southavong 10792* (L), EU623580 (Pruesapan et al., 2008), GQ503456, GQ503513, GQ503584; *Sauropus poomae* Welzen & Chayam., Chiang Rai, Thailand, *Phonsena et al.* 5245 (L), EU623582 (Pruesapan et al., 2008), GQ503457, GQ503515, GQ503586; *Sauropus quadrangularis* (Willd.) Müll.Arg., Chiang Mai, Thailand, *Maxwell 99-116* (L), EU623583 (Pruesapan et al., 2008), ---, ---, ---; *Sauropus “repens”* sp. nov., Thailand, *Middleton et al.* 2287 (L), GQ503385, ---, ---, GQ503566; *Sauropus rhamnoides* Blume, Chanthaburi, Thailand, *Esser 2001-4* (L),

EU623584 (Pruesapan et al., 2008), ---, ---, ---; *Sauropus similis* Craib, Chiang Mai, Thailand, *Larsen et al.* 46639 (L), GQ503399, GQ503462, GQ503520, GQ503592; *Sauropus spatulifolius* Beille, Honolulu, U.S.A., *Wong s.n.* (L), EU623588 (Pruesapan et al., 2008), ---, GQ503523, GQ503596; *Sauropus suberosus* Airy Shaw, Perak, Malaysia, *Chin 827* (L), EU623589 (Pruesapan et al., 2008), ---, ---, ---; *Sauropus thorelii* Beille, Chiang Mai, Thailand, *Van Welzen 2006-1* (L), EU623590 (Pruesapan et al., 2008), GQ503468, GQ503526, GQ503600; *Sauropus thyrsiflorus* Welzen, Kanchanaburi, Thailand, *Kostermans 765* (L), EU623591 (Pruesapan et al., 2008), GQ503469, GQ503527, GQ503601; *Sauropus villosus* (Blanco) Merr., Panay, Philippines, *Mcgregor 32398* (L), EU623593 (Pruesapan et al., 2008), ---, ---, ---; *Synostemon bacciformis* (L.) G.L.Webster, Northern Territory, Australia, *Cowie I 3418* (L), GQ503382, ---, GQ503502, ---, Bangkok, Thailand, *Pruesapan 2009-4* (L), ---, GQ503440, ---, ---; *Synostemon hirtellus* F.Muell., Queensland, Australia, *Bean 15558* (BRI), EU623573 (Pruesapan et al., 2008), GQ503447, GQ503508, GQ503574; *Synostemon "kakadu"* sp. nov., Australia, *Bruhl 1270* (NE), GQ503395, GQ503451, GQ503510, GQ503578; *Synostemon sphenophyllus* Airy Shaw, Queensland, Australia, *Gray 08597* (BRI), GQ503402, GQ503465, ---, GQ503597; *Synostemon "spinescens"* sp. nov., Australia, *Bean 20738* (NE), GQ503403, GQ503466, GQ503524, GQ503598; *Synostemon trachyspermus* (F.Muell.) Airy Shaw, Australia, *Bell 547* (NE), GQ503407, GQ503470, GQ503528, GQ503602.

b. Additional specimens of L herbarium used for morphological data matrix.

Species, locality, voucher number.

Notoleptopus decaisnei (Benth.) Voronts. & Petra Hoffm., Queensland, Australia, *Fraser 267*; *Flueggea virosa* (Roxb. ex Willd.) Voigt, Thailand, *Kerr 1116, 1444, 2015, 15372, Maxwell 71-467, 87-697, 89396*; *Glochidion benthamianum* Domin, Queensland, Australia, *Hyland 7949, 8648, 8668, 8922*. *Glochidion ferdinandi* (Müll.Arg.) Pax & Hoffm., Queensland, Australia, *Hyland 9056, 9062, 9134, Forster & Mc Dona 8174*; *Glochidion harveyanum* Domin, Queensland, Australia, *Forster & Tucker 5181, Forster et al. 21920, 24268, Bruhl & Gray 1110, Bruhl et al. 1127*; *Glochidion lobocarpum* (Benth.) F.M.Bailey, Queensland, Australia, *Forster 2198, Hyland 4368, 13778, 25652*; *Glochidion philippicum* (Cav.) C.B.Rob., Java, Indonesia, *Backer 29944, Wiradinata 284*, Papua New Guinea, *Carr 15899, 16429, Hoogland 5038*; *Phyllanthus acidus* (L.) Skeels, Borneo, Brunei, *Ashton BRUN 517*, Malaysia, *Stone 11947*, Thailand, *Maxwell 90-276, Van Welzen 2003-14, Watdahnahsahp 46*; *Phyllanthus amarus* Schumach. & Thonn., Laos, *Maxwell 98-183*, Thailand, *Kerr 1444, Maxwell 91-851, Phengkklai 224, Van Beusekom & Phengkklai 1228*; *Phyllanthus emblica* L., Thailand, *Maxwell 86-932, 87-959, 89-392, 90-276, Phusomsaeng 1967/27, B. Sangkhachand 3053*; *Phyllanthus mirabilis* Müll.Arg., Thailand, *Pooma et al. 2957, Smitinand & Sleumer 1128, 1332, Smitinand et al. 1096, 1138*; *Phyllanthus sauropodoideus* Airy Shaw, Queensland, *Forster & Booth 25417, Forster & Tucker 29857*.

Appendix 4.2. List of morphological characters used in the phylogenetic analysis.

Quantitative data: vegetative characters: 1-6, staminate characters: 7-12, pistillate characters: 13-20.

Qualitative data: vegetative characters: 21-34, staminate characters: 35-52, pistillate characters: 53-65.

1. Stipule length (mm). **2.** Stipule width (mm). **3.** Petiole length (mm). **4.** Leaf length (cm). **5.** Leaf width (cm). **6.** Vein number. **7.** Staminate diameter (mm). **8.** Staminate pedicel length (mm). **9.** Staminate sepal lobe length (mm). **10.** Staminate sepal lobe width (mm). **11.** Androphore length (mm). **12.** Anther length (mm). **13.** Pistillate pedicel length (mm). **14.** Pistillate calyx lobe length (mm). **15.** Pistillate calyx lobe width (mm). **16.** Stigma length (mm). **17.** Fruit height (mm). **18.** Fruit width (mm). **19.** Seed length (mm). **20.** Seed width (mm). **21.** Plant sexuality: (0) monoecious; (1) dioecious. **22.** Indumentum: (0) absent; (1) present. **23.** Blade shape: (0) orbicular; (1) oblong; (2) obovate; (3) elliptic; (4) ovate; (5) triangular. **24.** Blade texture: (0) papery; (1) chartaceous; (3) coriaceous. **25.** Leaf base symmetric: (0) asymmetric; (1) symmetric. **26.** Blade base: (0) emarginated; (1) truncate; (2) rounded to obtuse to acute; (3) cuneate to attenuate. **27.** Blade apex: (0) emarginate; (1) truncate; (2) rounded to obtuse to acute; (3) mucronate to acuminate to cuspidate. **28.** Wax papillae on abaxial leaf blade surface: (0) absent; (1) present. **29.** Real papillae on abaxial leaf blade surface: (0) absent; (1) present. **30.** Inflorescence position: (0) axillary; (1) cauliflorous to ramiflorous. **31.** Inflorescence type: (0) fascicle; (1) supra-axillary fascicle; (2) raceme or thyrse. **32.** Sex per inflorescence: (0) single; (1) both. **33.** Petal presence: (0) absent; (1) present. **34.** Sepal numbers: (0) 4 sepals; (1) 5 sepals; (2) 6 sepals. **35.** Staminate sepal connectivity: (0) free; (1) connate. **36.** Staminate sepal union: (0) basally; (1) halfway; (2) two third; (3) complete. **37.** Staminate calyx shape: (0) discoid; (1) campanulate to turbinate. **38.** Staminate sepal folding: (0) absent; (1) inwards; (2) outwards. **39.** Staminate sepal lobe shape: (0) lobes completely united; (1) obovate; (2) elliptic; (3) ovate; (4) triangular; (5) linear. **40.** Staminate lobe apex: (0) indistinct; (1) emarginate; (2) truncate; (3) rounded to obtuse; (4) acute; (5) acuminate. **41.** Staminate disc gland: (0) absent; (1) annular; (2) scales. **42.** Stamen number: (0) 2 stamens; (1) 3 stamens; (2) 4 stamens; (3) 6 stamens; (4) 7 stamens. **43.** Stamen connectivity: (0) free; (1) connate. **44.** Androphore branching: (0) unbranched; (1) branched. **45.** Anther position: (0) erect; (1) ascending; (2) horizontal. **46.** Filament connectivity: (0) free; (1) connate. **47.** Pollen shape: (0) suboblate; (1) oblate-spheroidal to spheroidal; (2) prolate; (3) prolate-spheroidal; (4) subprolate. **48.** Colpus type: (0) monoporate; (1) diploporate. **49.** Colpus numbers: (0) up to 4-colpi; (1) 5-8-colpi; (2) 9-14-colpi; (3) > 14-colpi. **50.** Colpus membrane: (0) smooth; (1) scabrate. **51.** Margo presence: (0) absent; (1) present. **52.** Pollen ornamentation: (0) reticulate; (1) micro-reticulate; (2) perforate; (3) regulate-reticulate; (4) bireticulate. **53.** Pistillate sepal equality: (0) unequal; (1) equal. **54.** Pistillate calyx connectivity: (0) free; (1) connate. **55.** Pistillate sepal shape: (0) obovate; (1) elliptic to rounded; (2) ovate; (3) triangular. **56.** Pistillate disc glands: (0) absent; (1) present. **57.** Rim of ovary: (0) absent; (1) present. **58.** Style presence: (0) absent; (1) present. **59.** Stigma apex: (0) entire; (1) bifid; (2) trifid. **60.** Stigma splitting: (0) \leq halfway; (1) >halfway. **61.** Stigma position: (0) erect; (1) ascending; (2) horizontal. **62.** Fruit type: (0) berry; (1) capsule; (2) drupe. **63.** Fruit grooved: (0) longitudinally; (1) not longitudinally. **64.** Seed sarcotesta: (0) absent; (1) present. **65.** Seed ornamentation (0) smooth; (1) ornamented.

Appendix 4.3. Morphological data matrix.

Taxon/character	1	2	3	4	5	6	7	8	9	10
<i>Notoleptopus decussisnei</i>	1.500-1.500	0.300-0.300	1.500-35.000	0.400-5.000	0.200-3.100	4.000-7.000	1.000-1.500	1.000-2.000	1.000-1.000	0.500-0.5000
<i>Flueggea virosa</i>	1.000-3.000	0.700-1.000	3.000-8.000	1.300-10.500	0.600-6.200	5.000-8.000	1.700-2.200	3.000-6.500	0.800-2.000	0.500-1.300
<i>Phyllanthus actidis</i>	0.500-1.300	0.300-1.000	1.500-2.500	1.800-10.000	1.300-4.500	3.000-9.000	2.300-2.300	0.800-2.000	1.000-1.500	0.800-1.300
<i>Phyllanthus amarus</i>	1.000-1.000	0.300-0.600	0.200-0.800	0.260-1.100	0.130-0.500	3.000-4.000	1.800-1.800	0.500-1.000	0.300-0.800	0.300-0.400
<i>Phyllanthus emblica</i>	0.300-1.000	0.600-0.600	0.200-0.800	0.500-1.200	0.150-0.250	4.000-6.000	3.500-3.500	1.500-3.000	1.200-2.000	0.400-1.000
<i>Phyllanthus mirabilis</i>	2.000-3.000	?	4.000-4.000	6.500-13.000	3.500-7.000	10.000-12.000	?	1.000-2.000	2.500-3.000	0.500-1.000
<i>Phyllanthus saurpodoides</i>	2.000-2.000	1.500-1.500	2.000-4.000	3.400-6.700	1.700-3.500	7.000-10.000	4.100-4.100	11.000-11.000	2.000-2.000	2.000-2.000
<i>Glochidion benthamicum</i>	1.000-1.200	0.800-0.800	3.000-4.000	2.000-7.000	1.100-2.700	8.000-9.000	4.000-4.000	10.500-10.500	2.000-2.000	1.200-1.200
<i>Glochidion ferdinandi</i>	1.800-1.800	1.500-1.500	2.000-3.000	2.600-7.600	1.000-2.500	8.000-9.000	3.300-3.300	11.000-11.000	2.100-2.200	1.000-1.500
<i>Glochidion harveyanum</i>	1.300-3.000	1.200-1.500	5.500-7.000	6.100-17.000	3.000-5.700	6.000-8.000	4.000-4.000	11.000-11.000	2.600-3.200	1.700-2.200
<i>Glochidion lobocarpum</i>	1.000-1.000	0.800-0.800	3.500-7.000	4.200-13.300	1.700-5.000	12.000-14.000	5.000-5.000	7.000-7.000	1.600-2.200	0.800-1.000
<i>Glochidion philippicum</i>	1.300-1.300	1.500-1.500	3.000-4.000	5.000-10.700	1.100-4.200	8.000-11.000	5.000-5.000	8.000-8.000	3.000-3.000	1.100-1.100
<i>Breyntia discigera</i>	1.000-2.000	0.300-0.700	2.000-3.000	2.500-5.500	1.000-2.500	5.000-6.000	?	1.500-3.000	?	?
<i>Breyntia glauca</i>	1.500-2.500	0.500-1.200	3.000-4.000	4.000-6.000	1.500-3.000	6.000-8.000	1.000-1.000	2.000-3.000	?	?
<i>Breyntia mollis</i>	1.000-2.000	1.000-1.000	2.500-3.500	4.000-7.500	2.500-4.500	6.000-7.000	2.000-2.000	2.000-2.000	2.000-2.000	2.000-2.000
<i>Breyntia "novoguineensis"</i>	1.500-2.000	0.750-0.750	2.000-3.000	3.000-6.500	2.000-3.000	7.000-8.000	?	1.500-2.000	?	?
<i>Breyntia oblongifolia</i>	1.000-2.000	0.500-1.200	2.000-2.500	2.000-3.000	1.000-1.500	5.000-6.000	1.000-1.000	1.000-2.000	1.000-1.000	1.000-2.000
<i>Breyntia retusa</i>	1.000-2.000	0.500-0.750	1.500-2.500	2.200-3.300	1.000-1.500	5.000-7.000	1.500-2.000	1.000-1.500	1.500-2.500	?
<i>Breyntia stipitata</i>	1.000-2.000	0.500-1.200	2.000-2.500	2.000-3.000	1.000-1.500	5.000-6.000	1.000-1.000	1.000-2.000	1.000-1.000	1.000-2.000
<i>Breyntia vestita</i>	1.000-1.250	0.500-0.500	2.000-2.500	1.500-3.500	0.800-2.200	4.000-6.000	1.250-1.250	1.500-1.500	?	?
<i>Sauropus amoebiflorus</i>	0.800-5.500	0.300-3.000	1.000-1.200	2.100-5.100	0.700-1.600	6.000-9.000	3.500-5.200	2.700-4.000	0.800-2.100	2.300-2.500
<i>Sauropus androgynus1</i>	3.000-4.000	?	2.000-3.000	4.000-6.000	1.500-3.500	4.000-8.000	3.000-5.000	3.000-3.500	0.500-1.500	0.600-2.000
<i>Sauropus androgynus2</i>	1.800-3.200	0.800-1.300	2.000-3.000	1.800-9.500	0.600-4.000	6.000-10.000	2.500-20.000	4.500-13.000	0.700-3.000	1.300-5.000
<i>Sauropus androgynus3</i>	1.800-3.200	0.800-1.300	2.000-3.000	1.800-9.500	0.600-4.000	6.000-10.000	2.500-20.000	4.500-13.000	0.700-3.000	1.300-5.000
<i>Sauropus assimilis</i>	1.000-1.000	0.500-0.500	3.000-4.000	2.500-4.700	1.200-2.000	5.000-6.000	12.000-22.000	6.000-6.000	2.500-5.000	0.500-1.200
<i>Sauropus asteranthos</i>	0.700-3.000	0.200-3.000	1.000-1.200	0.700-3.000	0.300-2.000	3.000-6.000	1.500-3.200	1.700-4.000	0.500-1.100	0.600-11.000
<i>Sauropus bicolor</i>	1.200-2.600	0.900-1.600	1.500-2.000	1.100-6.000	0.500-2.900	5.000-7.000	3.000-4.800	2.800-5.500	0.600-1.000	1.300-2.200
<i>Sauropus brevipes</i>	0.500-3.100	0.400-1.500	1.300-2.500	0.900-3.300	0.600-2.300	6.000-8.000	2.000-5.000	2.500-6.200	0.500-1.200	0.700-2.500
<i>Sauropus "carcosa"</i>	0.900-1.200	0.600-0.800	1.500-2.000	1.100-2.200	1.100-1.800	4.000-5.000	4.500-4.500	4.500-4.500	0.800-0.800	1.700-1.700
<i>Sauropus discocalyx</i>	2.500-3.000	2.000-2.500	2.500-4.000	11.500-17.500	5.800-7.200	12.000-15.000	12.000-13.000	13.500-15.000	1.000-1.500	4.500-4.500
<i>Sauropus garrettii</i>	2.500-4.200	0.300-1.200	2.000-3.000	1.700-12.800	1.100-4.200	8.000-12.000	4.000-6.500	5.000-15.000	0.500-0.800	1.200-2.500

Morphological data matrix. Continued.

Taxon/character	1	2	3	4	5	6	7	8	9	10
<i>Sauropus granulatus</i>	1.200-1.200	0.500-0.600	1.200-1.500	0.800-2.700	0.500-1.500	5.000-7.000	2.000-3.500	1.800-3.700	0.600-1.300	0.600-1.200
<i>Sauropus hirsutus</i>	1.800-4.000	0.700-2.000	1.700-2.800	1.400-7.700	1.000-3.800	5.000-9.000	1.500-4.000	1.400-4.300	0.400-1.800	0.600-1.300
<i>Sauropus kerrii</i>	0.700-2.500	0.300-0.800	1.000-1.000	0.520-1.200	0.300-0.700	4.000-6.000	2.600-3.200	2.000-4.200	0.600-1.200	1.000-1.300
<i>Sauropus "lithophila"</i>	0.200-0.200	0.500-0.500	1.500-2.000	1.500-3.700	0.900-2.800	7.000-8.000	4.000-4.000	5.000-5.000	0.200-0.200	2.500-2.500
<i>Sauropus macranthus</i>	2.300-8.500	1.300-2.800	3.000-5.000	3.800-20.000	1.900-8.200	10.000-17.000	2.500-4.500	7.500-15.000	0.500-1.200	1.000-2.000
<i>Sauropus micrasterias</i>	2.500-3.000	1.100-1.300	3.000-4.000	14.000-20.500	6.300-8.500	12.000-15.000	5.500-8.000	5.000-6.000	3.000-3.000	0.900-1.000
<i>Sauropus orbicularis</i>	0.700-1.200	0.500-0.800	1.400-1.500	0.600-3.000	0.350-2.300	5.000-6.000	1.800-2.300	2.300-5.200	0.200-0.400	0.700-1.000
<i>Sauropus poomae</i>	2.200-3.500	2.000-3.500	2.000-3.000	3.700-7.300	2.600-4.600	9.000-11.000	1.600-2.300	5.500-6.000	0.200-0.400	0.500-1.500
<i>Sauropus quadrangularis</i>	1.000-2.700	0.700-3.500	1.200-1.300	0.600-4.100	0.500-1.800	6.000-6.000	1.500-3.700	3.500-6.000	0.700-1.200	0.800-1.600
<i>Sauropus "repens"</i>	2.000-3.200	0.600-0.800	0.700-2.000	0.600-1.000	0.700-1.400	4.000-8.000	?	?	?	?
<i>Sauropus rhamnoides</i>	2.000-3.500	0.800-1.500	3.000-4.000	2.200-17.200	1.000-8.400	7.000-10.000	4.500-25.000	6.200-12.000	1.000-1.600	1.500-2.500
<i>Sauropus similis</i>	1.000-1.500	0.400-1.700	1.200-2.000	0.700-5.800	0.500-2.900	5.000-8.000	4.200-4.500	4.900-6.000	0.400-1.200	1.000-2.300
<i>Sauropus spatulifolius</i>	3.000-6.000	3.000-4.000	2.000-4.500	7.000-13.000	2.200-4.600	9.000-11.000	3.300-4.500	4.000-5.500	1.000-1.300	1.000-1.400
<i>Sauropus suberosus</i>	3.500-6.000	1.200-4.000	2.000-4.000	7.700-25.000	2.600-7.300	12.000-13.000	3.700-4.000	5.500-5.500	0.800-1.000	1.000-1.600
<i>Sauropus thorelii</i>	1.500-3.000	0.500-1.200	2.000-2.300	2.600-10.100	1.200-3.000	6.000-14.000	4.000-7.500	4.300-7.500	1.600-2.500	1.000-1.600
<i>Sauropus thysiflorus</i>	6.500-8.000	1.700-3.000	4.000-5.000	6.500-26.000	2.700-8.000	10.000-12.000	6.000-7.000	5.500-5.500	2.000-2.200	1.500-2.100
<i>Sauropus villosus</i>	1.300-4.000	0.200-0.500	1.200-2.000	1.000-6.500	0.600-1.900	9.000-13.000	1.000-3.000	1.200-4.000	1.200-1.200	0.400-0.400
<i>Synostemon bacciformis</i>	1.700-3.000	0.500-1.500	1.000-1.000	0.650-2.500	0.150-1.300	?	1.200-1.500	0.600-0.600	0.400-0.600	0.300-0.400
<i>Synostemon hirtellus</i>	0.500-1.400	?	0.300-1.800	0.650-3.400	0.150-1.250	?	?	0.900-10.000	1.800-3.000	1.000-1.000
<i>Synostemon "kakadu"</i>	0.300-0.500	?	0.800-1.200	0.600-1.500	0.200-0.700	?	?	1.500-2.000	2.700-3.200	1.200-1.200
<i>Synostemon sphenophyllus</i>	0.400-0.800	0.500-0.600	0.600-1.500	0.350-2.600	0.250-1.550	6.000-9.000	3.000-3.000	1.500-3.000	1.000-1.500	0.500-1.200
<i>Synostemon "spinescens"</i>	0.800-1.200	?	?	0.280-0.900	0.160-0.400	?	?	0.500-1.400	1.000-1.600	0.300-0.600
<i>Synostemon trachyspermus</i>	0.800-2.300	?	0.600-1.000	0.600-2.500	0.250-0.530	?	?	0.500-2.000	0.600-1.000	0.200-0.300
Taxon/character	11	12	13	14	15	16	17	18	19	20
<i>Notoleptopus decaisnei</i>	?	0.200-0.200	3.500-7.000	3.000-3.500	1.800-2.300	0.900-0.900	2.300-2.300	3.500-3.500	1.400-1.700	1.200-1.300
<i>Flueggea virosa</i>	?	0.300-0.500	1.500-5.000	0.800-2.000	0.500-1.300	0.500-1.000	4.000-5.000	4.000-5.000	2.200-2.500	1.700-1.800
<i>Phyllanthus acidus</i>	?	0.300-0.300	0.500-4.000	1.000-1.300	0.700-1.500	0.100-1.000	14.000-27.000	14.000-27.000	3.300-3.300	3.000-3.000
<i>Phyllanthus amarus</i>	0.100-0.300	0.300-0.300	1.700-1.700	0.800-0.800	0.500-0.500	0.100-0.300	1.300-1.300	1.800-1.800	0.900-0.900	0.700-0.700
<i>Phyllanthus emblica</i>	0.500-1.000	0.300-0.500	0.500-0.700	1.800-2.500	0.700-1.000	1.000-1.900	12.000-15.000	20.000-30.000	3.900-4.500	3.500-3.500
<i>Phyllanthus mirabilis</i>	?	0.600-0.800	2.000-3.000	4.000-5.500	2.000-2.500	0.800-1.000	?	?	?	?
<i>Phyllanthus sauropodoides</i>	0.0	0.200-0.200	9.000-9.000	2.200-3.000	2.000-3.000	1.000-1.000	5.000-5.000	6.800-6.800	3.800-3.800	2.500-2.500

Morphological data matrix. Continued.

Taxon/character	11	12	13	14	15	16	17	18	19	20
<i>Glochidion benthamianum</i>	1.200-1.200	0.800-0.800	6.000-6.000	1.100-1.100	?	1.200-1.200	5.000-5.000	9.000-9.000	4.000-4.000	3.000-3.000
<i>Glochidion ferdinandi</i>	2.000-2.000	0.800-0.800	1.800-1.800	0.500-1.100	0.400-0.600	2.000-2.000	7.000-7.000	11.000-21.000	3.800-3.800	3.800-3.800
<i>Glochidion harveyanum</i>	1.500-1.500	1.000-1.000	5.000-5.000	3.000-4.000	1.500-1.600	0.800-0.800	8.500-8.500	12.000-12.000	4.000-4.000	3.500-3.500
<i>Glochidion tobocarpum</i>	1.100-1.100	0.900-0.900	4.000-4.000	1.100-1.300	0.600-0.900	0.400-0.500	3.000-3.000	7.000-10.000	3.500-3.500	3.000-3.000
<i>Glochidion philippicum</i>	1.100-1.100	0.800-0.800	1.700-7.000	0.800-0.800	0.200-0.400	0.500-0.800	3.000-4.500	6.500-9.000	4.200-4.200	3.400-3.400
<i>Breyنيا discigera</i>	1.000-1.000	0.800-0.800	0.500-1.000	2.750-3.000	2.000-2.000	0.250-0.350	5.000-5.500	5.500-6.500	2.500-2.500	2.000-2.000
<i>Breyنيا glauca</i>	1.800-2.300	1.200-1.200	2.500-4.000	1.700-1.700	2.500-2.500	1.500-2.000	5.000-5.000	6.000-7.000	3.700-4.200	2.000-2.200
<i>Breyنيا mollis</i>	?	?	1.500-2.500	2.000-2.000	1.500-1.500	0.250-0.350	4.000-4.000	5.500-7.000	?	?
<i>Breyنيا "novoguineensis"</i>	?	?	1.200-1.500	2.500-3.000	?	2.000-3.000	4.000-5.000	2.600-2.600	2.600-2.600	1.200-1.200
<i>Breyنيا oblongifolia</i>	?	?	1.500-3.000	0.750-1.000	1.250-1.250	0.300-0.300	3.000-5.000	3.500-6.000	3.500-3.500	1.500-1.500
<i>Breyنيا retusa</i>	?	0.700-0.700	1.000-1.500	0.250-0.250	?	0.400-0.500	5.000-5.000	7.000-8.000	4.500-4.500	2.500-2.500
<i>Breyنيا stipitata</i>	?	?	1.500-3.000	0.750-1.000	1.250-1.250	0.300-0.300	3.000-5.000	3.500-6.000	3.500-3.500	1.500-1.500
<i>Breyنيا vestita</i>	?	?	3.000-4.000	0.500-0.500	1.000-1.000	0.200-0.200	3.500-4.000	4.000-5.000	?	?
<i>Sauropus amoebiflorus</i>	0.100-0.300	0.300-0.400	2.000-3.200	2.300-4.500	2.300-5.000	1.000-1.000	5.000-5.000	8.000-8.000	4.500-4.500	3.000-3.000
<i>Sauropus androgynus1</i>	0.300-0.300	0.200-0.200	?	?	?	?	15.000-15.000	17.000-17.000	?	?
<i>Sauropus androgynus2</i>	0.100-0.300	0.400-0.600	3.200-14.000	1.800-5.500	1.800-5.500	1.200-1.200	9.000-15.000	12.000-17.000	7.000-10.000	4.500-6.500
<i>Sauropus androgynus3</i>	0.100-0.300	0.400-0.600	3.200-14.000	1.800-5.500	1.800-5.500	1.200-1.200	9.000-15.000	12.000-17.000	7.000-10.000	4.500-6.500
<i>Sauropus assimilis</i>	1.000-1.000	1.300-1.300	2.500-3.000	0.500-0.500	0.250-0.250	?	?	?	?	?
<i>Sauropus asteranthos</i>	0.200-0.200	0.200-0.200	1.200-2.000	1.200-2.000	1.300-3.000	1.000-1.000	4.000-4.000	4.500-4.500	3.800-3.800	2.000-2.000
<i>Sauropus bicolor</i>	0.700-1.100	0.300-0.800	1.200-4.800	1.800-5.000	2.000-5.000	1.200-1.200	5.500-6.000	7.000-7.500	3.900-4.000	2.000-3.000
<i>Sauropus brevipes</i>	0.200-0.300	0.200-0.300	1.800-2.700	2.200-3.200	1.300-2.500	1.300-1.300	4.000-4.000	5.000-5.000	3.700-3.700	2.300-2.300
<i>Sauropus "carnosa"</i>	0.200-0.200	0.600-0.600	1.000-1.000	1.500-2.000	1.800-2.300	?	?	?	?	?
<i>Sauropus discocalyx</i>	0.300-0.300	0.300-0.300	13.000-13.000	5.000-5.000	3.000-3.000	2.000-2.000	?	?	?	?
<i>Sauropus garrettii</i>	0.100-0.400	0.400-0.700	3.800-13.000	2.000-5.000	1.000-3.100	2.000-2.000	7.000-8.000	9.000-11.000	5.800-7.000	3.800-4.000
<i>Sauropus granulosus</i>	0.800-0.800	0.800-0.900	1.800-2.800	1.300-2.500	1.100-3.000	2.000-2.000	5.000-5.000	7.000-7.000	3.700-4.000	2.000-3.000
<i>Sauropus hirsutus</i>	0.200-0.300	0.300-0.300	2.400-7.000	2.200-13.000	1.400-4.500	1.400-1.400	5.000-8.000	5.000-8.000	5.000-5.000	2.700-2.700
<i>Sauropus kerrii</i>	0.500-1.000	0.700-1.100	1.000-1.500	1.300-2.200	1.800-3.000	2.100-2.100	7.000-7.000	3.500-3.500	3.200-3.200	3.000-3.000
<i>Sauropus "lithophila"</i>	0.200-0.200	0.600-0.600	1.000-1.000	1.400-1.800	1.800-2.300	?	?	?	?	?
<i>Sauropus macranthus</i>	0.200-0.200	0.300-0.300	30.000-65.000	2.200-5.300	2.200-3.100	2.000-2.000	10.000-13.000	17.000-22.000	10.000-10.500	6.500-8.000
<i>Sauropus micranthias</i>	0.300-0.300	0.500-0.500	2.200-2.200	2.000-2.500	1.300-1.300	1.000-1.000	?	?	?	?
<i>Sauropus orbicularis</i>	0.200-0.200	0.200-0.200	1.300-2.200	1.200-2.000	1.200-2.300	1.000-1.000	5.000-5.000	6.000-6.500	3.500-3.500	2.200-2.200
<i>Sauropus poomae</i>	0.300-0.300	0.400-0.500	0.800-1.000	1.200-1.600	1.000-1.600	1.000-1.002	?	?	?	?

Morphological data matrix. Continued.

Taxon/character	11	12	13	14	15	16	17	18	19	20
<i>Sauropus quadrangularis</i>	0.300-0.300	0.300-0.300	1.500-4.300	1.200-2.500	1.500-2.200	1.000-1.003	4.000-4.000	5.000-5.500	3.500-3.500	2.000-2.000
<i>Sauropus "repens"</i>	?	?	4.300-4.300	1.400-1.800	1.800-2.300	?	?	?	?	?
<i>Sauropus rhamnoides</i>	0.100-0.400	0.300-0.500	7.500-20.000	4.000-16.000	3.300-11.000	2.300-2.300	13.000-23.000	13.000-31.000	11.000-11.000	6.000-7.000
<i>Sauropus similis</i>	0.200-0.200	0.300-0.300	1.500-3.700	1.000-2.100	1.000-3.300	1.000-1.000	3.500-4.200	5.500-5.500	3.000-3.300	2.100-2.300
<i>Sauropus spatulifolius</i>	0.300-0.300	0.300-0.300	4.000-5.500	2.000-2.500	1.200-1.800	0.700-0.700	5.500-5.500	7.000-7.000	?	?
<i>Sauropus suberosus</i>	0.200-0.200	0.400-0.500	2.500-4.500	1.200-3.000	2.000-4.200	1.300-1.300	?	?	?	?
<i>Sauropus thorelii</i>	0.200-0.700	0.400-0.400	2.000-7.000	1.100-3.500	1.200-3.300	1.200-1.200	4.000-4.000	7.000-7.000	?	?
<i>Sauropus thyrsoiflorus</i>	0.200-0.300	0.400-0.400	3.000-6.000	4.800-6.000	3.300-4.000	2.000-2.000	15.000-15.000	19.000-19.000	14.000-14.000	8.000-8.000
<i>Sauropus villosus</i>	0.200-0.200	0.600-0.700	0.700-2.500	0.400-1.300	0.500-1.300	1.200-1.200	4.000-6.000	8.000-11.000	4.500-5.500	3.000-4.000
<i>Synostemon bacciformis</i>	0.200-0.200	0.200-0.200	3.000-4.000	2.000-2.800	1.000-1.400	0.500-0.500	5.000-6.500	5.000-5.200	4.500-4.900	1.200-1.800
<i>Synostemon hirellus</i>	?	1.700-2.400	0.800-6.000	0.800-1.500	?	0.300-0.900	5.900-9.000	4.000-6.700	5.000-7.200	?
<i>Synostemon "kakaadu"</i>	?	1.500-1.500	1.000-1.000	3.000-3.200	1.600-1.600	1.200-1.200	7.400-9.000	6.200-7.000	6.000-7.200	2.500-3.200
<i>Synostemon sphenophyllus</i>	1.300-1.300	0.800-0.800	1.500-4.500	1.800-5.500	1.400-2.400	1.000-1.000	5.200-5.600	5.500-5.800	4.000-5.500	2.500-3.000
<i>Synostemon "spinescens"</i>	?	0.800-1.200	1.400-2.600	1.200-1.800	0.300-0.500	?	3.000-4.500	3.000-4.500	4.000-4.800	3.000-3.000
<i>Synostemon trachyspermus</i>	?	0.200-0.400	0.200-3.000	0.800-2.000	0.300-1.200	0.200-0.600	4.500-6.500	4.500-6.500	4.000-5.200	1.600-2.000

Taxon/character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
<i>Notoleptopus decaisnei</i>	0	1	0,3	1	1	3	2	0	0	0	0	0	1	1	0	?	0	0	1,2	4	1	2
<i>Flueggea virosa</i>	1	0	2,3	0	1	2,3	2	0	0	0	0	0	0	1	0	?	0	0	2,3	3,4	1	2
<i>Phyllanthus acidus</i>	0	0	4	0	0	2	3	0	0	0	0	1	0	0	0	?	0	0	1,2	4	1	1
<i>Phyllanthus amarus</i>	0	0	1,2	0	0	2	2,3	0	0	0	0	1	0	1	0	?	0	0	2,3	4	1	0
<i>Phyllanthus emblica</i>	0	0,1	1	2	0	0	2	0	0	0	0	1	0	2	0	?	0	0	1,2	3	1	0
<i>Phyllanthus mirabilis</i>	0	0	1	2	0	0	2	0	?	0	0	1	0	1	0	?	0	0	2	5	1	3
<i>Phyllanthus sauropodoides</i>	0	0	4	0	0	3	2,3	0	0	0	0	1	0	2	0	?	0	0	2	3	1	4
<i>Glochidion benthamianum</i>	0	1	3	2	0	2,3	3	0	0	0	0	1	0	2	0	?	0	0	2,3	3,4	0	0
<i>Glochidion ferdinandi</i>	0	0	4	2	0	3	3	0	0	0	0	0	0	2	0	?	0	0	2	4	0	0
<i>Glochidion harveyanum</i>	0	1	5	2	0	3	3	0	0	0	0	1	0	2	0	?	0	0	2	4	0	0
<i>Glochidion lobocarpum</i>	0	1	7	2	0	3	3	1	0	0	0	1	0	2	0	?	0	0	2	3	0	0
<i>Glochidion philippicum</i>	0	1	3,4	2	0	2	3	0	0	0	0	0	0	2	0	?	0	0	2	3	0	0
<i>Breynia discigera</i>	0	1	3,4	1	1	2	2	1	0	0	0	0	0	2	1	3	1	0	?	?	2	0
<i>Breynia glauca</i>	0	0	3,4	1	1	2	2	1	0	0	0	0	0	2	1	3	1	0	?	3,4	2	0
<i>Breynia mollis</i>	0	1	3,4	1	1	2	2,3	0	0	0	0	0	0	2	1	3	1	0	?	?	2	0
<i>Breynia "novoguineensis"</i>	0	1	3	0	1	2	2	?	0	0	0	0	0	2	1	3	1	0	?	?	2	0

Morphological data matrix. Continued.

Taxon/character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
<i>Breynia oblongifolia</i>	0	0	3,4	1,2	1	2	0,2	1	0	0	0	0	0	2	1	3	1	0	?	?	2	0
<i>Breynia retusa</i>	0	0	1,3	0,1	1	2	5	1	0	0	0	0	0	2	1	3	1	0	?	3,4	2	0
<i>Breynia stipitata</i>	0	0	3,4	1,2	1	2	0,2	1	0	0	0	0	0	2	1	3	1	0	?	3,4	2	0
<i>Breynia vestita</i>	0	1	1,3	1	1	2	0,2	1	0	0	0	0	0	2	1	3	1	0	?	3	2	0
<i>Sauropus amoebiflorus</i>	0	0	3,4	1	1	3	2	0	0	0	0	1	0	2	1	1	0	0	4	1	2	0
<i>Sauropus androgynus1</i>	0	0	4	0	1	1,2	2	0	0	0	0	1	0	2	1	3	0	2	4	4	2	0
<i>Sauropus androgynus2</i>	0	0	4	0	1	1,2	2	0	0	0	0	1	0	2	1	3	0	0	0	0,1	2	0
<i>Sauropus androgynus3</i>	0	0	4	0	1	1,2	2	0	0	0	0	1	0	2	1	3	0	0	0	0,1	2	0
<i>Sauropus assimilis</i>	0	0	4	0	1	3	2,3	0	0	0	0	1	0	2	1	0	0	0	5	3	2	0
<i>Sauropus asteranthos</i>	0	0	2,3	0	0	1,3	2	0	1	0	0	1	0	2	1	1	0	0	4	1	2	0
<i>Sauropus bicolor</i>	0	0	4	2	0	0,2	2	0	1	0	0	0	0	2	1	1	0	0	3	1,3	2	0
<i>Sauropus brevipes</i>	0	0	2,4	0,1	1	0,3	2	0	1	0	0	0	0	2	1	1	0	0	3	1,3	2	0
<i>Sauropus "carnosa"</i>	0	0	0,3,4	2	1	0	0,2	0	0	0	0	0	0	2	1	2	0	0	4	1	2	0
<i>Sauropus discocalyx</i>	0	0	3,4	0	1	3	3	0	0	1	2	0	0	2	1	3	0	0	4	3	2	0
<i>Sauropus garrettii</i>	0	0	3,4	0	1	2	3	0	1	0	0	0	0	2	1	3	0	0	4	3	2	0
<i>Sauropus granulosus</i>	?	0	2	1	1	3	1,2	0	1	0	0	0	0	2	1	0	0	1	2	1,3	0	0
<i>Sauropus hirsutus</i>	0	1	3	0,1	1	2,3	2	0	0	0	0	1	0	2	1	0	0	0	2	4	2	0
<i>Sauropus kerrii</i>	1	0	2	1	1	2,3	1,2	0	0	0	0	0	0	2	1	0	0	1	1	1,3	0	0
<i>Sauropus "lithophila"</i>	0	1	4	2	1	1,2	2	0	1	0	0	0	0	2	1	3	0	0	3	0	2	0
<i>Sauropus macranthus</i>	0	0	3,4	0	1	3	3	0	0	0	0	1	0	2	1	1	0	0	4	1,3	2	0
<i>Sauropus micrasterias</i>	0	0	3	0	1	3	3	0	0	1	2	1	0	2	1	0	0	0	4	3	2	0
<i>Sauropus orbicularis</i>	0	0	0,2	0,1	1	3	2	0	1	0	0	1	0	2	1	3	0	0	3	3	2	0
<i>Sauropus poomae</i>	0	0	4,5	0	1	1	2	0	0	0	2	1	0	2	1	3	0	0	3	3	2	0
<i>Sauropus quadrangularis</i>	0	0,1	2,3	0,1	0	1,3	0,2	0	1	0	0	1	0	2	1	0	0	0	1	1,3	2	0
<i>Sauropus "repens"</i>	0	1	0,3	2	1	1	2	0	2	0	0	0	0	2	1	3	0	0	?	3	2	0
<i>Sauropus rhamnoides</i>	0	0	3,4	0	0	3	3	0	1	0	0	0	0	2	1	3	0	0	4	3	2	0
<i>Sauropus similis</i>	0	0	3,4	0,1	1	0,3	2	0	0	0	0	0	0	2	1	1	0	0	2	3	2	0
<i>Sauropus spatulifolius</i>	0	0	2	1	1	2	0	0	0	1	2	0	0	2	1	1	0	0	2,4	3	2	0
<i>Sauropus suberosus</i>	0	1	2,3	0	1	3	2,3	0	0	1	2	0	0	2	1	2	0	0	2	3	2	0
<i>Sauropus thoretii</i>	0	0	3,4	0	1	3	2,3	0	0	1	2	0	0	2	1	0	0	0	2	1	2	0
<i>Sauropus thyrsoflorus</i>	0	0	3	0	1	3	3	0	0	1	2	0	0	2	1	1	0	0	4	4	2	0
<i>Sauropus villosus</i>	0	1	4	0	0	0,3	2	0	1	0	0	1	0	2	1	0	0	0	2	3	2	0
<i>Synostemon baeciformis</i>	0	0	3	2	1	2	2	0	1	0	0	0	0	2	1	1	0	0	3	3	2	0
<i>Synostemon hirtellus</i>	1	0,1	2,3	?	1	2	3	?	?	0	?	0	0	2	1	2	1	0	?	3	0	0

Morphological data matrix. Continued.

Taxon/character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
<i>Synostemon "kakadu"</i>	1	1	2,3	?	1	2	3	?	?	0	?	0	0	2	0	?	1	0	1	3	0	0
<i>Synostemon sphenophyllus</i>	0	0	2,3	1	1	2	3	0	1	0	0	0	0	2	1	1	1	0	1	3	0	0
<i>Synostemon "spinescens"</i>	1	?	2	?	1	2	3	?	?	0	0	0	0	2	0	?	1	1	2	?	0	0
<i>Synostemon trachyspermus</i>	0	0	2,3	?	1	2	3	?	?	0	?	1	0	2	0	?	0	0	2	3	0	0
<i>Notoleptopus decaisnei</i>	0	?	0	0	2	?	?	?	?	12	1	0	1	1	?	0	?	0	1	1	0	1
<i>Flueggea virosa</i>	0	?	0	0	4	0	0	1	1	0,2	1	0	1,2	1	0	1	2	0	2	0	1	0
<i>Phyllanthus acidus</i>	0	?	0	0	1	1	0	?	?	3	1	0	2	1	0	1	1	0	2	1	0	0
<i>Phyllanthus amarus</i>	1	?	1	1	3,4	1	0	?	?	4	1	0	1	1	0	1	1	0	1	1	0	1
<i>Phyllanthus emblica</i>	1	?	0	1	4	0	0	?	?	0	1	0	0	1	0	1	1	0	2	1	0	0
<i>Phyllanthus mirabilis</i>	1	?	0	1	1	0	0	?	?	0,2	1	0	1,2	1	0	1	1	0	1	1	?	?
<i>Phyllanthus sauropodoides</i>	1	?	0	1	?	?	?	?	?	?	0	0	2	1	0	1	0	?	0	1	1	0
<i>Glochidion benthamianum</i>	1	0	0	?	1	0	0	0	0	0	1	0	1,2	0	1	0	?	0	1	0	0	0
<i>Glochidion ferdinandi</i>	1	0	0	?	?	?	?	?	?	?	0	0	3	0	1	0	?	0	1	0	0	0
<i>Glochidion harveyanum</i>	1	0	0	?	?	?	?	?	?	?	0	0	1	0	1	0	?	0	1	0	0	0
<i>Glochidion lobocarpum</i>	1	0	0	?	?	?	?	?	?	?	0	0	2	0	1	0	?	0	1	0	0	0
<i>Glochidion philippicum</i>	1	0	0	?	3	0	0	?	?	?	0	2	0	0	1	0	?	0	1	0	0	0
<i>Breyenia discigera</i>	1	0	0	1	0	1	1	0	0	0	1	1	?	0	1	0	0	0	0	1	1	0
<i>Breyenia glauca</i>	1	0	0	1	0	1	2	0	0	0	1	1	?	0	0	0,1	0	0	0	1	1	0
<i>Breyenia mollis</i>	1	0	0	1	?	?	?	?	?	?	1	1	?	0	0	?	?	0	0	1	1	0
<i>Breyenia "novoguineensis"</i>	1	0	0	1	?	?	?	?	?	?	1	1	?	0	0	?	?	0	0	1	1	0
<i>Breyenia oblongifolia</i>	1	0	0	1	0	1	1	0	0	0	1	1	?	0	0	1	0	0	0	1	1	0
<i>Breyenia retusa</i>	1	0	0	1	0	1	2	0	0	1	1	1	?	0	1	1	0	0	0	1	1	0
<i>Breyenia stipitata</i>	1	0	0	1	0	1	1	0	0	0	1	1	?	0	0	1	0	0	0	1	1	0
<i>Breyenia vestita</i>	1	0	0	1	0	1	1	0	0	0	1	1	?	0	0	1	0	0	0	1	1	0
<i>Sauropus amoebiflorus</i>	1	1	2	1	1	1	2	0	1	0	0	2	0	1	0	1	1	2	1	1	0	0
<i>Sauropus androgynus1</i>	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Sauropus androgynus2</i>	1	1	2	1	1	1	2	0	1	0,1	0	0	0	0	0	1	1	2	1	1	0	0
<i>Sauropus androgynus3</i>	1	1	2	1	1	1	2	0	1	0,1	0	0	0	0	0	1	1	2	1	1	0	0
<i>Sauropus assimilis</i>	1	1	2	1	1	1	2	0	1	1	0	0	0	0	0	1	1	2	?	?	?	?
<i>Sauropus asteranthos</i>	1	1	2	1	1	1	2	0	1	0	0	0	0	1	0	1	1	2	1	1	0	0

Morphological data matrix. Continued.

Taxon/character	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
<i>Sauropus bicolor</i>	1	1	2	1	1	1	2	0	1	0	1	0	0	0	1	0	1	1	2	1	1	0	0
<i>Sauropus brevipes</i>	1	1	2	1	1	1	2	0	1	0	0	0	0,1	0	1	0	1	0	2	1	1	0	0
<i>Sauropus "carcosa"</i>	1	1	2	1	?	?	?	?	?	?	0	0	0	0	0	0	1	1	2	?	?	?	?
<i>Sauropus discocalyx</i>	1	1	2	1	1	1	3	0	1	1	1	0	0	0	0	0	1	1	2	?	1	?	?
<i>Sauropus garrettii</i>	1	1	2	1	1	1	3	0	1	1	0	0	0,2	0	0	0	1	1	2	1	1	0	0
<i>Sauropus granulatus</i>	1	1	1	1	1	1	2	0	1	1,2	0	0	0	0	1	0	1	1	1	1	1	0	0
<i>Sauropus hirsutus</i>	1	1	2	1	0	1	2	0	1	1	0	0	0,1	0	1	0	1	1	2	1	1	0	1
<i>Sauropus kerrii</i>	1	1	1	1	4	1	1	0	1	2	1	0	0	0	1	0	1	1	1	1	1	0	0
<i>Sauropus "lithophila"</i>	1	1	2	1	?	?	?	?	?	?	0	0	0,1	0	0	0	1	1	2	?	?	?	?
<i>Sauropus macranthus</i>	1	1	2	1	3	1	2	0	1	0,1	0	0	1,2	0	0	0	1	1	2	1	1	0	0
<i>Sauropus micrasterias</i>	1	1	2	1	1	1	2	0	1	1	0	0	0	0	0	0	1	1	2	?	1	?	?
<i>Sauropus orbicularis</i>	1	1	2	1	1	1	2	0	1	0	1	0	0	0	1	0	1	0	2	1	1	0	0
<i>Sauropus poomae</i>	1	1	2	1	?	?	?	?	?	?	1	0	1,2	0	0	0	1	1	2	?	1	?	?
<i>Sauropus quadrangularis</i>	1	1	2	1	1	1	2	0	1	1	1	0	0,1	0	1	0	1	1	1	1	1	0	1
<i>Sauropus "repens"</i>	1	?	2	?	?	?	?	?	?	?	0	0	1	0	0	0	1	1	2	?	?	?	?
<i>Sauropus rhamnoides</i>	1	1	2	1	1	1	2	0	1	0,1	0	0	0	0	0	0	1	1	2	1	1	0	0
<i>Sauropus similis</i>	1	1	2	1	1	1	2	0	1	1	1	0	0	0	1	0	1	1	2	1	1	0	0
<i>Sauropus spatulifolius</i>	1	1	2	1	3	1	2	0	1	1	1	0	0	0	0	0	1	1	2	1	1	?	?
<i>Sauropus suberosus</i>	1	1	2	1	3	1	2	0	1	1	0	0	0	0	0	0	1	0	2	?	1	?	?
<i>Sauropus thoretii</i>	1	1	2	1	1	1	3	0	1	1	0	0	0,2	0	0	0	1	0	2	1	1	?	?
<i>Sauropus thysiflorus</i>	1	1	2	1	1	1	2	0	1	1	0	0	1	0	0	0	1	1	2	1	1	0	0
<i>Sauropus villosus</i>	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0	0	1	1	2	1	1	0	0
<i>Synostemon bacciformis</i>	1	0	0	1	0	1	1	0	1	1	1	0	2	0	1	0	1	0	0	1	1	0	1
<i>Synostemon hirtellus</i>	1	0	0	1	1	1	0	0	0	0,2	1	0	?	0	?	0	1	?	0	1	1	0	1
<i>Synostemon "kakaadu"</i>	1	0	0	1	1	1	0	0	0	0	1	0	0	0	?	0	1	0	0	1	1	0	0
<i>Synostemon sphenophyllus</i>	1	0	0	1	1	1	1	0	0	1	1	0	0	0	?	0	1	0	0	1	1	0	1
<i>Synostemon "spinescens"</i>	1	0	0	1	?	?	?	?	?	?	1	0	0,1	0	?	0	1	0	0	1	1	0	1
<i>Synostemon trachyspermus</i>	1	0	0	1	1	1	1	0	0	1	1	0	1,2	0	?	0	1	0	0	1	1	0	1

