



Phylogenetic reconstruction prompts taxonomic changes in *Sauropus*, *Synostemon* and *Breynia* (*Phyllanthaceae* tribe *Phyllanthaeae*)

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Abstract Previous molecular phylogenetic studies indicated expansion of *Breynia* with inclusion of *Sauropus* s.str. (excluding *Synostemon*). The present study adds qualitative and quantitative morphological characters to molecular data to find more resolution and/or higher support for the subgroups within *Breynia* s.lat. However, the results show that combined molecular and morphological characters provide limited synergy. Morphology confirms and makes the infrageneric groups recognisable within *Breynia* s.lat. The status of the *Sauropus androgynus* complex is discussed. Nomenclatural changes of *Sauropus* species to *Breynia* are formalised. The genus *Synostemon* is reinstated.

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INTRODUCTION

A phylogenetic analysis of tribe *Phyllanthaeae* (*Phyllanthaceae*) using DNA sequence data by Kathriarachchi et al. (2006) provided a backbone phylogeny for *Phyllanthus* L. and related genera. Their study recommended subsuming *Breynia* L. (including *Sauropus* Blume), *Glochidion* J.R.Forst. & G.Forst., and *Synostemon* F.Muell. into *Phyllanthus* as they rendered that genus paraphyletic. In practice, only Chakrabarty & Balakrishnan (2009) and Wagner & Lorence (2011) have published new combinations under *Phyllanthus*. Later, Chakrabarty & Balakrishnan (2012) reverted to the recognition of *Breynia* at generic rank probably because of Pruesapan et al. (2012).

We subscribe to the use of monophyly as a criterion for recognition of supraspecific taxa, but we prefer to do this for smaller and recognisable groups instead of an unrecognisable and unmanageable 'giant' *Phyllanthus*. Our studies (Pruesapan et al. 2012, Telford et al. unpubl. data) have found morphological synapomorphies that define *Synostemon* and *Breynia* (including *Sauropus*). We treat these genera as our working hypotheses of monophyly, and as justified as the alternative hypothesis of a 'giant' *Phyllanthus*. The latter is only based on the undersampling of 95 species of > 1 250 species (Kathriarachchi et al. 2006). Because of the undersampling the backbone phylogeny precludes the split up of *Phyllanthus* into monophyletic and recognisable taxa. Our taxonomic approach is perhaps not satisfactory at the moment, but results in fewer nomenclatural rearrangements than when a 'giant' *Phyllanthus* is adhered to, also because already 42 generic names (see synonymy in Webster 1994, Radcliffe-Smith 2001) are available for subclades of *Phyllanthus*.

Sauropus in the strict sense (excluding *Synostemon*; Pruesapan et al. 2008, 2012) and *Breynia* are two closely related tropical Asian-Australian genera with up to 52 and 35 species, respectively (Webster 1994, Govaerts et al. 2000a, b, Radcliffe-Smith 2001). *Sauropus* comprises mainly herbs and shrubs, whereas species of *Breynia* are always shrubs. Both genera share bifid or emarginate styles, non-apiculate anthers, smooth seeds and they generally possess sepal scales. However, they differ in features of their staminate calyx and androecium (Webster 1994, Radcliffe-Smith 2001). The staminate flowers have often been used to characterise species in *Sauropus*, whereas the pistillate organs are quite distinct in *Breynia*.

The close relationship between *Breynia* and *Sauropus* was noted by several authors (Croizat 1940, Airy Shaw 1980a, b, 1981a), but they never united the genera. The last complete revision of *Breynia* was made by Müller Argoviensis (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 1).

Table 1 Numbers of species of *Sauropus* s.str. (without *Synostemon*) and *Breynia* s.str. in different regions of Asia.

Genus	Author(s)	Region	Species
<i>Sauropus</i> s.str.	Beille (1927)	Indochina	22
	Airy Shaw (1969, 1972, 1975, 1981a)	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> s.str.	Li (1994), Li et al. (2008)	China	5
	Chakrabarty & Gangopadhyay (1996)	India	4
	Van Welzen & Esser (2005)	Thailand	7
	Thin (2007)	Vietnam	15

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

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Table 2 Airy Shaw's traditional classification of *Sauropus* s.str. (without *Synostemon*) compared with the results of the phylogenetic analysis. Names in *italics* are still in the same position, those in straight characters are absent from the other column; in **bold** the very different position of *Sa. spatulifolius* Beille (for other authorities see Table 3).

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

confirmed in recent molecular studies (Kathriarachchi et al. 2006, Pruesapan et al. 2008, 2012).

Several infrageneric classifications were proposed for *Sauropus* s.str. (Müller Argoviensis 1863, 1866, Hooker 1887, Pax & Hoffmann 1922, Beille 1927, Airy Shaw 1969, Li 1987, Thin 2007). Airy Shaw's classification (1969), based on Müller Argoviensis (1863, 1866) and Pax & Hoffmann (1922), is the most accepted one with the distinction of five sections: *Sauropus*, *Cryptogynium* ('*Ceratogynium*') Müll.Arg., *Hemisauropus* Müll. Arg., *Schizanthi* Pax & K.Hoffm. and *Glochidioidei* Airy Shaw (Table 2). Unfortunately, it is obvious 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, 2012) only very partly agrees with the infrageneric classification by Airy Shaw (1969). Only two clades with combinations of the sections could be recognised (summary in Fig. 1).

A subdivision of *Breynia* (s.str.) has never been published. However, Müller Argoviensis (1866), in the last complete revision, separated the species into two genera, *Melanthesopsis* Müll. Arg. and *Breynia*. *Melanthesopsis* included two species with an enlarged calyx in staminate flowers and relatively large and distinctly divided stigmas in pistillate flowers, whereas species of his *Breynia* shared an often small calyx in staminate and small and less distinctly split stigmas. *Melanthesopsis* is now

regarded as synonym of *Breynia* (Webster 1994, Radcliffe-Smith 2001), although the two species groups are still well recognisable morphologically.

DNA sequence data have resolved phylogenetic relationships of numerous plant groups. Yet, the inclusion of morphological data in phylogenetic analysis is desirable for several reasons: Morphology often helps to construct more robust estimates of phylogeny (De Queiroz et al. 1995). Morphology may provide a 'reality check' of the molecular results and morphology is necessary to resolve the phylogenetic relationships of fossil taxa (Wiens 2004, and references therein). Finally, morphology is inevitable for the study of 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* form a monophyletic group, with a monophyletic *Breynia* nested within a paraphyletic *Sauropus* (Kathriarachchi et al. 2006, Pruesapan et al. 2008, 2012.). The group has two clades; one has a part of *Sauropus* plus *Breynia* and the other only contains species of *Sauropus* (Group A and B in Fig. 1, respectively). To date, the purely *Sauropus* group is mainly unresolved (Pruesapan et al. 2008, 2012). The inclusion of morphological data in phylogenetic analyses may provide better resolved relationships within the group.

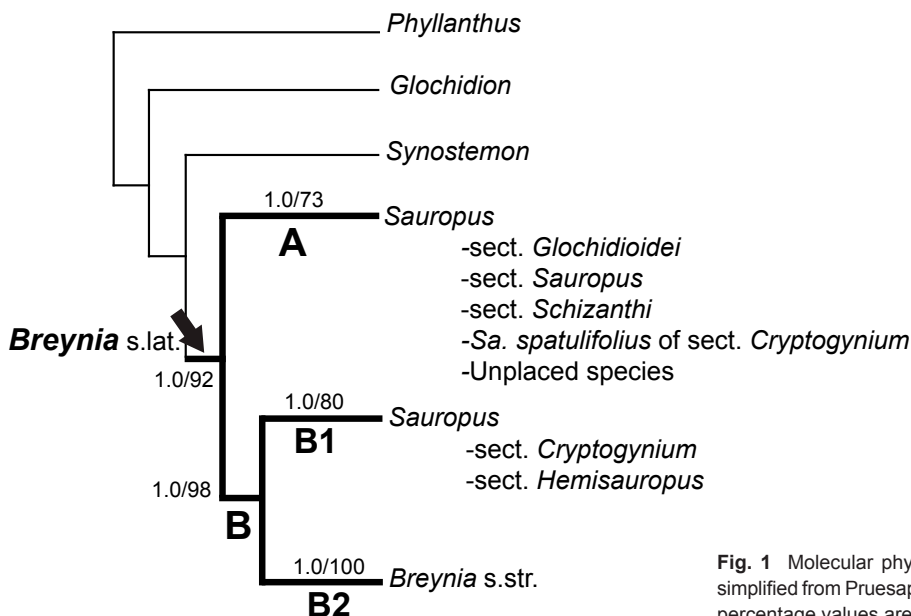


Fig. 1 Molecular phylogenetic relationships of *Breynia* s.lat. (bold lines) simplified from Pruesapan et al. (2012). The posterior probabilities / bootstrap percentage values are indicated on the branches.

Table 3 Voucher information for the molecular and morphological data for this study. The GenBank accession numbers, origin and herbarium can be found in Pruesapan et al. (2012). In this study only one representative sample was used per taxon (*Sa. androgynus* excepted), the non-*Breynia/Sauropus* genera are represented by only a few species, and for morphology, if descriptions were lacking, additional specimens, referred here, were sampled. In Fig. 3–5, ^a indicated as *Sa. androgynus*1, ^b indicated *Sa. androgynus*2, and ^c indicated as *Sa. androgynus*3. Three representatives of *Sauropus* s.str. (without *Synostemon*), already published under *Breynia*, are placed alphabetically among the appropriate *Sauropus* samples.

Ingroups — *Breynia* species: Subg. *Breynia* sect. *Breynia*: *B. discigera* Müll.Arg.: Takeuchi et al. 18873; *B. glauca* Craib: Pooma et al. 2702; *B. mollis* J.J.Sm.: Sands 1076; *B. 'novoguineensis'* sp. nov. (Esser & Stuppy unpubl.): Baker et al. 37; *B. oblongifolia* (Müll.Arg.) Müll.Arg.: Forster 32745; *B. retusa* (Dennst.) Alston: Soejarto & Southavong 10783; *B. stipitata* Müll.Arg.: Bruhl 2478; *B. vestita* Warb.: Barker & Beaman 70. Subg. *Breynia* sect. *Cryptogynium*: *Sauropus amoebiflorus* Airy Shaw: Kerr 19655; *Sa. asteranthos* Airy Shaw: Esser 99-13; *Sa. bicolor* Craib: Esser 99-21; *Sa. brevipes* Müll.Arg.: Middleton et al. 974; *Sa. granulatus* Airy Shaw: Pooma et al. 4257; *Sa. hirsutus* Beille: Larsen et al. 33993; *Sa. kerrii* Airy Shaw: Van Beusekom & Phengklai 1065; *Sa. orbicularis* Craib: Soejarto & Southavong 10792; *Sa. quadrangularis* (Willd.) Müll.Arg.: Maxwell 99-116; *Sa. similis* Craib: Larsen et al. 46639. Subg. *Sauropus*: *Sa. androgynus* (L.) Merr.: ^aKathriarachchi et al., ^bTelford & Bruhl 13056, ^cVan Welzen 2006-4; *Sa. assimilis* Thwaites: Kostermans 27871; *B. carnososa* Welzen & Pruesapan: Middleton et al. 4070; *Sa. discocalyx* Welzen: Beusekom & Phengklai 566; *Sa. garrettii* Craib: Sino-American Guizhou Botanical Expedition 1872; *B. lithophila* Welzen & Pruesapan: Phonsena et al. 5594; *Sa. macranthus* Hassk.: Telford & Bruhl 13107; *Sa. micrasterias* Airy Shaw: Erwin & Chai S 27479; *Sa. poomae* Welzen & Chayam.: Phonsena et al. 5245; *B. repens* Welzen & Pruesapan: Middleton et al. 2287; *Sa. rhamnoides* Blume: Esser 2001-4; *Sa. spatulifolius* Beille: Wong s.n.; *Sa. suberosus* Airy Shaw.: Chin 827; *Sa. thorelii* Beille: Van Welzen 2006-1; *Sa. thyrsiflorus* Welzen: Kostermans 765; *Sa. villosus* (Blanco) Merr.: BS (Mcgregor) 32398. *Glochidion* species: *G. benthamianum* Domin, molecular: Bruhl 1026, morphology: Australia, Queensland, Hyland 7949, 8648, 8668, 8922 (all L); *G. ferdinandi* (Müll.Arg.) Pax & Hoffm., molecular: Bruhl 2457, morphology: Australia, Queensland, Forster & McDonald 8174, Hyland 9056, 9062, 9134 (all L); *G. harveyanum* Domin, molecular: Bruhl 2527, morphology: Australia, Queensland, Bruhl & Gray 1110, Bruhl et al. 1127, Forster & Tucker 5181, Forster et al. 21920, 24268 (all L); *G. lobocarpum* (Benth.) F.M.Bailey, molecular: Bruhl 1146, morphology: Australia, Queensland, Forster 2198, Hyland 4368, 13778, 25652 (all L); *G. philippicum* (Cav.) C.B.Rob., molecular: Forster 29379, morphology: Indonesia, Jawa Timur, Backer 29944, Wiradinata 284, Papua New Guinea, Carr 15899, 16429, Hoogland 5038 (all L). *Phyllanthus* species: *P. acidus* (L.) Skeels, molecular: Van Welzen 2003-14, morphology: Brunei, Ashton BRUN 517, Malaysia, Stone 11947, Thailand, Maxwell 90-276, Van Welzen 2003-14, Watdahnahsahp 46 (all L); *P. amarus* Schumacher & Thonn., molecular: Van Welzen 2006-5, morphology: Laos, Maxwell 98-183, Thailand, Kerr 1444, Maxwell 91-851, Phengklai 224, Van Beusekom & Phengklai 1228 (all L); *P. emblica* L., molecular: Van Welzen 2003-11, morphology: Thailand, Maxwell 86-932, 87-959, 89-392, 90-276, Phusomsaeng 1967/27, B. Sangkhachand 3053 (all L); *P. mirabilis* Müll.Arg., molecular: Sirichamorn YSM 2009-05, morphology: Thailand, Pooma et al. 2957, Smitinand & Sleumer 1128, 1332, Smitinand et al. 1096, 1138 (all L); *P. sauropodoides* Airy Shaw, molecular: Forster 29857, morphology: Australia, Queensland, Forster & Booth 25417, Forster & Tucker 29857. *Synostemon* species: *Sy. bacciformis* (L.) G.L.Webster: Cowie I 3418, Pruesapan 2009-4; *Sy. hirtellus* F.Muell.: Bean 15558; *Sy. 'kakadu'* sp. nov.: Bruhl 1270; *Sy. sphenophyllus* Airy Shaw: Gray 08597; *Sy. 'spinescens'* sp. nov.: Bean 20738; *Sy. trachyspermus* (F.Muell.) Airy Shaw: Bell 547. **Outgroups — *Flueggea virosa*** (Roxb. ex Willd.) Voigt, molecular: Larsen et al. 45328, morphology: Thailand, Kerr 1116, 1444, 2015, 15372, Maxwell 71-467, 87-697, 89-396 (all L); *Notoleptopus decaisnei* (Benth.) Voronts. & Petra Hoffm.: Fraser 267.

Our aims are to:

- i. clarify the phylogenetic relationships within *Breynia* s.lat. (*Breynia* combined with *Sauropus*) based on a combination of molecular and morphological data;
- ii. provide a new generic circumscription and infrageneric classification for *Breynia* s.lat.;
- iii. provide nomenclature changes where needed.

MATERIALS AND METHODS

Taxon sampling

Twenty three species, based on Pruesapan et al. (2012), 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* (11 species; including three new species of *Sauropus*, which were published already under *Breynia*: *B. carnososa* Welzen & Pruesapan, *B. lithophila* Welzen & Pruesapan and *B. repens* Welzen & Pruesapan; Van Welzen & Pruesapan 2010), *Glochidion* (five species), *Phyllanthus* (five species), *Synostemon* (six species) and two outgroup taxa.

The type of *Sauropus* (*Sa. androgynus* (L.) Merr. as accepted name) was included, the type of *Breynia*, *B. disticha* J.R.Forst. & G.Forst., was not included as our sample did not yield DNA; the species was included in the *matK* and ITS analyses of Kathriarachchi et al. (2006) and Pruesapan et al. (2008). In those analyses, *B. disticha* was a member of a strongly supported clade with the other samples of *Breynia*. The type of sect. *Cryptogynium* (*Sa. rigidus* Thwaites) and that of *Hemisauropus* (*Sa. rostratus* Miq.) were also not present in the molecular analyses, but morphologically comparable species were included.

Molecular data

The molecular dataset is similar to that used in Pruesapan et al. (2012), in which aligned sequences of four DNA markers (*accD-psal* IGS, ITS1-5.8S-ITS2, *PHYC*, *trnS-trnG* IGS) were used. However, the sample has been reduced to a single

specimen for every *Breynia/Sauropus* species (except for *Sa. androgynus* because of problems with the circumscription) and far fewer species of the related genera. Table 3 gives an overview of the material studied, also the material used for morphological data. The aligned sequences of 3 578 base pairs are available upon request from the authors.

Morphological data

The same species used for the molecular analyses were also used to obtain morphological data. The lists of voucher specimens, morphological characters and the morphological data matrix are presented in Table 3–5, respectively. 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 et al. 2000, Van Welzen 2003, Esser & Stuppy unpubl. data). Relevant specimens at L were examined for some characters that were not indicated in the literature. As much as possible specimens used in the revisions by Van Welzen et al. (2000), Van Welzen (2003) and Esser & Stuppy (unpubl. data) were sampled. The characters of *Synostemon* were taken from Telford et al. (unpubl. data), and from representative specimens. The characters of *Glochidion* were taken from representative specimens only, the characters of *Phyllanthus* were scored from Chantharanonthai (2007) in combination with specimens, and for the outgroups, we used Vorontsova & Hoffmann (2008) in combination with additional material for *Notoleptopus decaisnei* (Benth.) Voronts. & Petra Hoffm., while the data of *Flueggea virosa* (Willd.) Voigt were obtained from specimens (see Table 3). All pollen characters were recorded from Sagun & Van der Ham (2003) and Webster & Carpenter (2008).

Coding of morphological data

At first, 20 continuous, quantitative and 45 discrete, qualitative morphological characters of 54 taxa were coded for the analysis. These characters were selected because either they were already used for recognition of supraspecific taxa or they

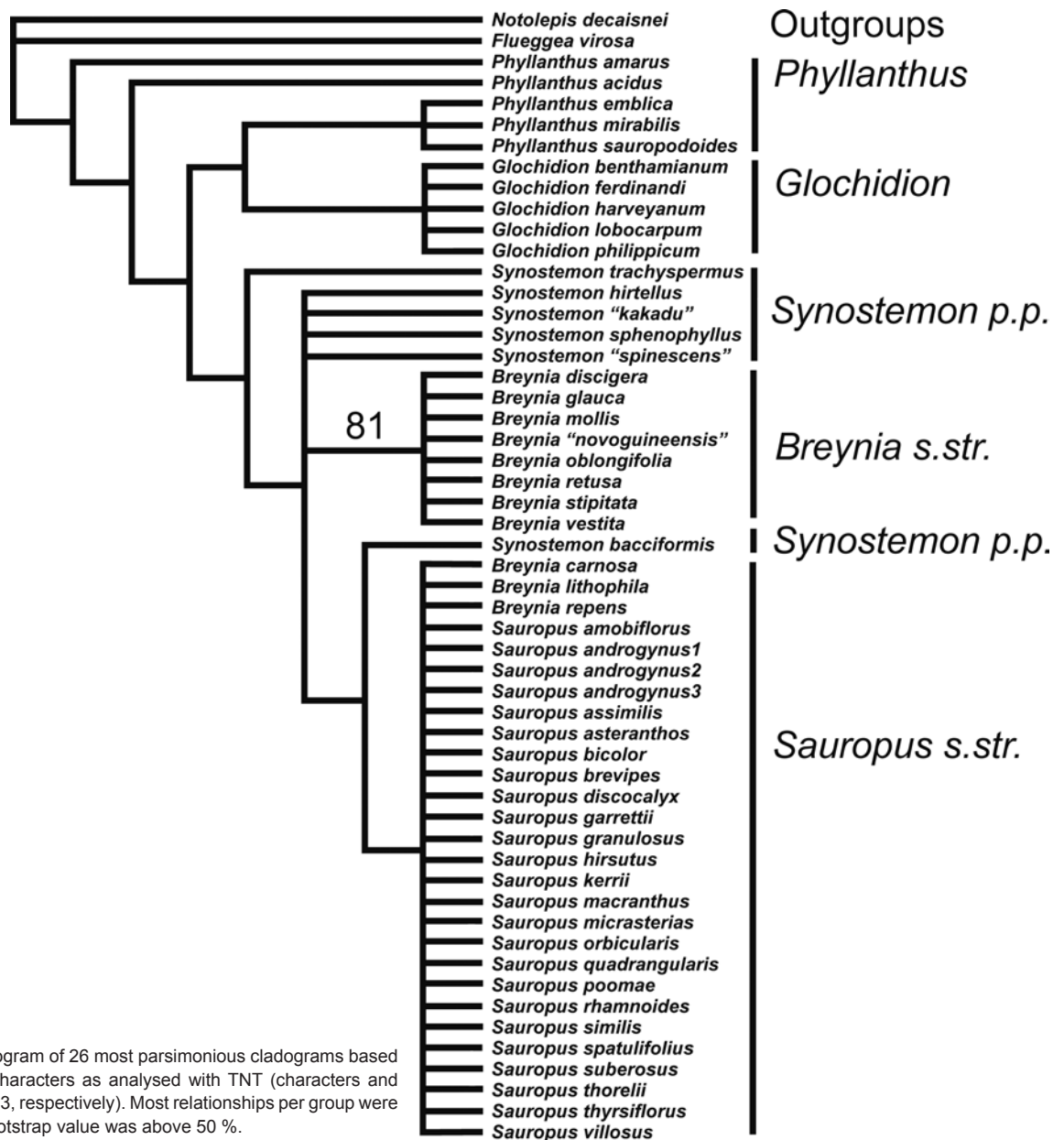


Fig. 2 Consensus cladogram of 26 most parsimonious cladograms based on only morphological characters as analysed with TNT (characters and matrix in Appendix 2 and 3, respectively). Most relationships per group were polytomies. Only one bootstrap value was above 50 %.

showed great variation, which could be divided into discrete states where it concerned the qualitative characters. In principle all characters that fulfilled these criteria were coded, because we did not want to make a-priori selections. In a first parsimony analysis the continuous characters showed little or no phylogenetic signal, and for further analysis, only six quantitative characters were retained that could be recoded in discrete states on basis of gaps in the measurements for most species. These were combined with the qualitative characters, giving a total of 51 morphological characters that were analysed (Table 4). The data matrix is shown in Table 5. All data were treated as unordered and of equal weight.

Phylogenetic analyses

The analyses were conducted under Maximum Parsimony (MP) and Bayesian Inference (BI). MP cladograms were analysed with TNT (Tree analysis using New Technology) version 1.1 (Goloboff et al. 2008), using 100 random replicates and TBR. Bootstrapping was done 1 000 times under the same settings.

For BI, the morphological data and each of the molecular markers were used as different partitions; for the morphological data as model rates = gamma was used, for the molecular data rates = invgamma nst = 6. The analyses were conducted with

MrBayes v. 3.2.2 (Ronquist et al. 2012), using three times two runs, each initiated with a random tree and with four Markov chains per run composed of one cold and three heated chains, with the temperature parameter T set to 0.05 to ensure good mixing. Each analysis ran for 120 million generations, which were sampled every 1 000 generations. The program Tree-annotator v.1.7.5 (Drummond & Rambaut 2007) was used to calculate six Maximum Clade Credibility (MCC) trees, one for each run. Tracer v. 1.4 (Rambaut & Drummond 2007) was used to check if all parameters showed effective sampling sizes (ESS) exceeding 200, which indicates that they are a good representation of the posterior distributions. Posterior probability values (PP; Ronquist & Huelsenbeck 2003) were added to the 50 %-majority rule consensus cladogram. Mesquite v. 2.72 (build 527) (Maddison & Maddison 2009) was used to trace the character evolution.

RESULTS

The MP analysis of morphological data only resulted in 70 cladograms of 256 steps. The strict consensus cladogram is summarized in Fig. 2. Most groups appeared as polytomies. The diagram shows a somewhat closer relationship between *Syno-*

Table 4 List of morphological characters used in the phylogenetic analysis.

Quantitative data: vegetative character: 1, staminate characters: 2–3, pistillate and fruit characters: 4–6.

Qualitative data: vegetative characters: 7–20, staminate characters: 21–38, pistillate characters: 39–51.

Character 52, leaf lengths in cm, has been added to show the variation among the species in Fig. 4a.

1. Maximum leaf length (cm) 1 = ≤ 6.5 2 = ≥ 7	19. Petal presence 0 = absent 1 = present	34. Colpus type 0 = monoporate 1 = diploporate
2. Maximum diameter staminate flowers (mm) 1 = < 10 2 = ≥ 10	20. Sepal numbers 0 = 4 sepals 1 = 5 sepals 2 = 6 sepals	35. Colpus numbers 0 = up to 4-colpi 1 = 5–8-colpi 2 = 9–14-colpi 3 = > 14-colpi
3. Length androphore (mm) 1 = ≤ 0.4(–0.7) 2 = 0.5–2.3	21. Staminate sepal connectivity 0 = free 1 = connate	36. Colpus membrane 0 = smooth 1 = scabrate
4. Length pistillate calyx lobes (mm) 1 = ≤ 5 2 = > 5	22. Staminate sepal union 0 = basally 1 = halfway 2 = two-third 3 = complete	37. Margo presence 0 = absent 1 = present
5. Fruit width (and length) (mm) 1 = 1.3–9 (1–11) 2 = 9–27 (11–21)	23. Staminate calyx shape 0 = discoid 1 = campanulate to turbinate	38. Pollen ornamentation 0 = reticulate 1 = micro-reticulate 2 = perforate 3 = regulate-reticulate 4 = bireticulate
6. Seed width (mm) 1 = ≤ 4 mm 2 = > 2 mm	24. Staminate sepal folding 0 = absent 1 = inwards 2 = outwards	39. Pistillate sepal equality 0 = unequal 1 = equal
7. Plant sexuality 0 = monoecious 1 = dioecious	25. Staminate sepal lobe shape 0 = lobes completely united 1 = obovate 2 = elliptic 3 = ovate 4 = triangular 5 = linear	40. Pistillate calyx connectivity 0 = free 1 = connate
8. Indumentum 0 = absent 1 = present	26. Staminate sepal lobe apex 0 = indistinct 1 = emarginate 2 = truncate 3 = rounded to obtuse 4 = acute 5 = acuminate	41. Pistillate sepal shape 0 = obovate 1 = elliptic to rounded 2 = ovate 3 = triangular
9. Blade shape 0 = orbicular 1 = oblong 2 = obovate 3 = elliptic 4 = ovate 5 = triangular	27. Staminate disc glands 0 = absent 1 = annular 2 = scales	42. Pistillate disc glands 0 = absent 1 = present
10. Blade texture 0 = papery 1 = chartaceous 2 = coriaceous	28. Stamen number 0 = 2 stamens 1 = 3 stamens 2 = 4 stamens 3 = 6 stamens 4 = 7 stamens	43. Ovary rim 0 = absent 1 = present
11. Leaf base symmetry 0 = asymmetric 1 = symmetric	29. Stamen connectivity 0 = free 1 = connate	44. Style presence 0 = absent 1 = present
12. Blade base 0 = emarginate 1 = truncate 2 = rounded to obtuse to acute 3 = cuneate to attenuate	30. Androphore branching 0 = unbranched 1 = branched	45. Stigma apex 0 = entire 1 = bifid 2 = trifid
13. Blade apex 0 = emarginate 1 = truncate 2 = rounded to obtuse to acute 3 = mucronate to acuminate to cuspidate	31. Anther position 0 = erect 1 = ascending 2 = horizontal	46. Stigma splitting 0 = ≤ halfway 1 = > halfway
14. Wax papillae on abaxial leaf blade surface 0 = absent 1 = present	32. Filament connectivity 0 = free 1 = connate	47. Stigma position 0 = erect 1 = ascending 2 = horizontal
15. Real papillae on abaxial leaf blade surface 0 = absent 1 = present	33. Pollen shape 0 = suboblate 1 = oblate-spheroidal to spheroidal 2 = prolate 3 = prolate-spheroidal 4 = subprolate	48. Fruit type 0 = berry 1 = capsule 2 = drupe
16. Inflorescence position 0 = axillary 1 = cauliflorous to ramiflorous		49. Fruit grooves 0 = longitudinal 1 = not longitudinal
17. Inflorescence type 0 = fascicle 1 = supra-axillary fascicle 2 = raceme or thyrses		50. Seed sarcotesta 0 = absent 1 = present
18. Sexes per inflorescence 0 = single 1 = both		51. Seed ornamentation 0 = smooth 1 = ornamented

[52. Leaf lengths in cm; only used in Fig. 4a]

Table 5 Morphological data matrix with quantitative (1–6) and qualitative (7–51) characters. Added is column 52 with the variation in length (in cm) of the species as used in Fig. 4a. Three species, published already under *Breynia*, but part of *Sauropus* s.str. (without *Synostemon*) are placed under *Sauropus*.

Taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Notoleptopus decaisnei</i>	1	1	?	1	1	1	0	1	0,3	1	1	3	2	0	0	0	0	0	1	1	0	?	0	0	1,2	4	1
<i>Flueggea virosa</i>	2	1	?	1	1	1	1	0	2,3	0	1	2,3	2	0	0	0	0	0	0	1	0	?	0	0	2,3	3,4	1
<i>Phyllanthus acidus</i>	2	1	?	1	2	1	0	0	4	0	0	2	3	0	0	0	0	1	0	0	0	?	0	0	1,2	4	1
<i>Phyllanthus amarus</i>	1	1	1	1	1	1	0	0	1,2	0	0	2	2,3	0	0	0	0	1	0	1	0	?	0	0	2,3	4	1
<i>Phyllanthus emblica</i>	1	1	2	1	2	1	0	0,1	1	2	0	0	2	0	0	0	0	1	0	2	0	?	0	0	1,2	3	1
<i>Phyllanthus mirabilis</i>	2	?	?	2	?	?	0	0	1	2	0	0	2	0	?	0	0	1	0	1	0	?	0	0	2	5	1
<i>Phyllanthus sauropodooides</i>	1	1	0	1	1	1	0	0	4	0	0	3	2,3	0	0	0	0	1	0	2	0	?	0	0	2	3	1
<i>Glochidion benthamianum</i>	2	1	2	1	1	1	0	1	3	2	0	2,3	3	0	0	0	0	1	0	2	0	?	0	0	2,3	3,4	0
<i>Glochidion ferdinandi</i>	2	1	2	1	2	1	0	0	4	2	0	3	3	0	0	0	0	0	0	2	0	?	0	0	2	4	0
<i>Glochidion harveyanum</i>	2	1	2	1	2	1	0	1	5	2	0	3	3	0	0	0	0	1	0	2	0	?	0	0	2	4	0
<i>Glochidion lobocarpum</i>	2	1	2	1	1	1	0	1	3	2	0	3	3	1	0	0	0	1	0	2	0	?	0	0	2	3	0
<i>Glochidion philippicum</i>	2	1	2	1	1	1	0	1	3,4	2	0	2	3	0	0	0	0	0	0	2	0	?	0	0	2	3	0
<i>Breynia discigera</i>	1	?	2	1	1	1	0	1	3,4	1	1	2	2	1	0	0	0	0	0	2	1	3	1	0	?	?	2
<i>Breynia glauca</i>	1	1	2	1	1	1	0	0	3,4	1	1	2	2	1	0	0	0	0	0	2	1	3	1	0	?	3,4	2
<i>Breynia mollis</i>	2	1	?	1	1	?	0	1	3,4	1	1	2	2,3	0	0	0	0	0	0	2	1	3	1	0	?	?	2
<i>Breynia 'novoguineensis'</i>	1	?	?	1	1	1	0	1	3	0	1	2	2	?	0	0	0	0	0	2	1	3	1	0	?	?	2
<i>Breynia oblongifolia</i>	1	1	?	1	1	1	0	0	3,4	1,2	1	2	0,2	1	0	0	0	0	0	2	1	3	1	0	?	3,4	2
<i>Breynia retusa</i>	1	1	?	1	1	1	0	0	1,3	0,1	1	2	5	1	0	0	0	0	0	2	1	3	1	0	?	3,4	2
<i>Breynia stipitata</i>	1	1	?	1	1	1	0	0	3,4	1,2	1	2	0,2	1	0	0	0	0	0	2	1	3	1	0	?	3,4	2
<i>Breynia vestita</i>	1	1	?	1	1	?	0	1	1,3	1	1	2	0,2	1	0	0	0	0	0	2	1	3	1	0	?	3	2
<i>Sauropus amoebiflorus</i>	1	1	1	1	1	1	0	0	3,4	1	1	3	2	0	0	0	0	1	0	2	1	1	0	0	4	1	2
<i>Sauropus androgynus1</i>	1	1	1	?	2	?	0	0	4	0	1	1,2	2	0	0	0	0	1	0	2	1	3	0	2	4	4	2
<i>Sauropus androgynus2</i>	2	2	1	2	2	2	0	0	4	0	1	1,2	2	0	0	0	0	1	0	2	1	3	0	0	0	0,1	2
<i>Sauropus androgynus3</i>	2	2	1	2	2	2	0	0	4	0	1	1,2	2	0	0	0	0	1	0	2	1	3	0	0	0	0,1	2
<i>Sauropus assimilis</i>	1	2	2	1	?	?	0	0	4	0	1	3	2,3	0	0	0	0	1	0	2	1	0	0	0	5	3	2
<i>Sauropus asteranthos</i>	1	1	1	1	1	1	0	0	2,3	0	0	1,3	2	0	1	0	0	1	0	2	1	1	0	0	4	1	2
<i>Sauropus bicolor</i>	1	1	2	2	1	1	0	0	4	2	0	0,2	2	0	1	0	0	0	0	2	1	1	0	0	3	1,3	2
<i>Sauropus brevipes</i>	1	1	1	1	1	1	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
<i>Breynia carnososa</i>	1	1	1	1	?	?	0	0	0,3,4	2	1	0	0,2	0	0	0	0	0	0	2	1	2	0	0	4	1	2
<i>Sauropus discocalyx</i>	2	2	1	2	?	?	0	0	3,4	0	1	3	3	0	0	1	2	0	0	2	1	3	0	0	4	3	2
<i>Sauropus garrettii</i>	2	1	1	2	1	1	0	0	3,4	0	1	2	3	0	1	0	0	0	0	2	1	3	0	0	4	3	2
<i>Sauropus granulatus</i>	1	1	2	1	1	1	?	0	2	1	1	3	1,2	0	1	0	0	0	0	2	1	0	0	1	2	1,3	0
<i>Sauropus hirsutus</i>	2	1	1	2	1	1	0	1	3	0,1	1	2,3	2	0	0	0	0	1	0	2	1	0	0	0	2	4	2
<i>Sauropus kerrii</i>	1	1	2	1	1	1	1	0	2	1	1	2,3	1,2	0	0	0	0	0	0	2	1	0	0	1	1	1,3	0
<i>Breynia lithophila</i>	1	1	1	1	?	?	0	1	4	2	1	1,2	2	0	1	0	0	0	0	2	1	3	0	0	3	0	2
<i>Sauropus macranthus</i>	2	1	1	2	2	2	0	0	3,4	0	1	3	3	0	0	0	0	1	0	2	1	1	0	0	4	1,3	2
<i>Sauropus micrasterias</i>	2	1	1	1	?	?	0	0	3	0	1	3	3	0	0	1	2	1	0	2	1	0	0	0	4	3	2
<i>Sauropus orbicularis</i>	1	1	1	1	1	1	0	0	0,2	0,1	1	3	2	0	1	0	0	1	0	2	1	3	0	0	3	3	2
<i>Sauropus poomae</i>	2	1	1	1	?	?	0	0	4,5	0	1	1	2	0	0	0	2	1	0	2	1	3	0	0	3	3	2
<i>Sauropus quadrangularis</i>	1	1	1	1	1	1	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
<i>Breynia repens</i>	1	?	?	1	?	?	0	1	0,3	2	1	1	2	0	2	0	0	0	0	2	1	3	0	0	?	3	2
<i>Sauropus rhamnoides</i>	2	2	1	2	2	2	0	0	3,4	0	0	3	3	0	1	0	0	0	0	2	1	3	0	0	4	3	2
<i>Sauropus similis</i>	1	1	1	1	1	1	0	0	3,4	0,1	1	0,3	2	0	0	0	0	0	0	2	1	1	0	0	2	3	2
<i>Sauropus spatulifolius</i>	2	1	1	1	1	?	0	0	2	1	1	2	0	0	0	1	2	0	0	2	1	1	0	0	2,4	3	2
<i>Sauropus suberosus</i>	2	1	1	1	?	?	0	1	2,3	0	1	3	2,3	0	0	1	2	0	0	2	1	2	0	0	2	3	2
<i>Sauropus thorelii</i>	2	1	1	1	1	?	0	0	3,4	0	1	3	2,3	0	0	1	2	0	0	2	1	0	0	0	2	1	2
<i>Sauropus thyrsiflorus</i>	2	1	1	2	2	2	0	0	3	0	1	3	3	0	0	1	2	0	0	2	1	1	0	0	4	4	2
<i>Sauropus villosus</i>	1	1	1	1	1	1	0	1	4	0	0	0,3	2	0	1	0	0	1	0	2	1	0	0	0	2	3	2
<i>Synostemon bacciformis</i>	1	1	1	1	1	1	0	0	3	2	1	2	2	0	1	0	0	0	0	2	1	1	0	0	3	3	2
<i>Synostemon hirtellus</i>	1	?	?	1	1	?	1	0,1	2,3	?	1	2	3	?	?	0	?	0	0	2	1	2	1	0	?	3	0
<i>Synostemon 'kakadu'</i>	1	?	?	1	1	1	1	1	2,3	?	1	2	3	?	?	0	?	0	0	2	0	?	1	0	1	3	0
<i>Synostemon sphenophyllus</i>	1	1	2	2	1	1	0	0	2,3	1	1	2	3	0	1	0	0	0,1	0	2	1	1	1	0	1	3	0
<i>Synostemon 'spinescens'</i>	1	?	?	1	1	1	1	?	2	?	1	2	3	?	?	0	0	0	0	2	0	?	1	1	2	?	0
<i>Synostemon trachyspermus</i>	1	?	?	?	1	1	0	0	2,3	?	1	2	3	?	?	0	?	1	0	2	0	?	0	0	2	3	0

stemon and *Sauropus* than between *Breynia* and *Sauropus*. The morphology of the androecium of *Sy. bacciformis* and *Sauropus* is also similar; this is the reason why Airy Shaw (1980b) united *Sauropus* s.str. and *Synostemon*. *Glochidion* and *Breynia* are morphologically distinct.

All ESS values of the BI analyses of the morphological and molecular data were checked with Tracer; all priors were much higher than 200, only the Alpha1 prior was below 200 (c. 150). Therefore, the resulting cladograms are deemed trustworthy. The six MCC trees were equal in the major lineages, but varied in Group A and B1. Fig. 3 shows an MCC tree in which *B. carnososa* is basal in clade A, but in other MCC trees it is located as sister to *B. lithophila*. The variation among the MCC trees for Group A and B1 does not influence our conclusions, therefore we continue with one MCC tree, the one shown in Fig. 3–5. In Fig. 3 most morphological characters are parsimoni-

ously plotted on the MCC tree. Several characters (3, 9, 12, 13, 18, 25, 26, 33, 37, 38, 41) were left out because of many homoplasies, polymorphic species and unknown values, so that it was impossible to reliably optimise the changes in these characters. Several characters deserve special attention (see discussion) and these are presented in Fig. 4 (1: leaf length; 43: ovary rim) and in Fig. 5 (31: anther position; 21: staminate sepal connectivity; 22: staminate sepal union; 23: staminate flower shape; 27: staminate disc glands; 47: stigma position).

The results of the BI analysis (Fig. 3) correspond highly with the cladogram solely based on molecular data (Pruesapan et al. 2012), because molecular data make up the majority of our dataset. The MCC tree (Fig. 3) shows of course far more resolution than the 50 %-majority rule cladogram in Pruesapan et al. (2012: f. 2), but the posterior probabilities for comparable branches tend to be a bit lower, probably because of high

28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	
2	0	?	0	0	2	?	?	?	?	1,2	1	0	1	1	?	0	0	?	0	1	1	0	1	0.4–5	
2	0	?	0	0	4	0	0	1	1	0,2	1	0	1,2	1	0	1	2	0	2	0	1	0	1	1.3–10.5	
1	0	?	0	0	1	1	0	?	?	3	1	0	2	1	0	1	1	0	0	2	1	0	0	1.8–10	
0	1	?	1	1	3,4	1	0	?	?	4	1	0	1	1	0	1	1	0	0	1	1	0	1	0.26–1.1	
0	1	?	0	1	4	0	0	?	?	0	1	0	0	1	0	1	1	1	0	2	1	0	0	0.5–1.2	
3	1	?	0	1	1	0	0	?	?	0,2	1	0	1,2	1	0	1	1	0	0	1	1	?	?	6.5–13	
4	1	?	0	1	?	?	?	?	?	?	0	0	2	1	0	1	0	?	0	1	1	0	0	3.4–6.7	
0	1	0	0	?	1	0	0	0	0	0	1	0	1,2	0	0	1	0	?	0	1	0	0	0	2–7	
0	1	0	0	?	?	?	?	?	?	?	0	0	3	0	0	1	0	?	0	1	0	0	0	2.6–7.6	
0	1	0	0	?	?	?	?	?	?	?	0	0	1	0	0	1	0	?	0	1	0	0	0	6.1–17	
0	1	0	0	?	?	?	?	?	?	?	0	0	2	0	0	1	0	?	0	1	0	0	0	4.2–13.3	
0	1	0	0	?	3	0	0	0	0	0	1	0	2	0	0	1	0	?	0	1	0	0	0	5.0–10.7	
0	1	0	0	1	0	1	1	0	0	0	1	1	?	0	1	0	0	0	0	0	1	1	0	2.5–5.5	
0	1	0	0	1	0	1	2	0	0	0	1	1	?	0	0	0	0,1	0	0	0	1	1	0	4–6	
0	1	0	0	1	?	?	?	?	?	?	1	1	?	0	0	0	1	0	0	0	1	1	0	4–7.5	
0	1	0	0	1	?	?	?	?	?	?	1	1	?	0	0	?	?	?	?	0	0	1	1	0	3–6.5
0	1	0	0	1	0	1	1	0	0	0	1	1	?	0	0	0	1	0	0	0	1	1	0	2–3	
0	1	0	0	1	0	1	2	0	0	1	1	1	?	0	0	1	1	0	0	0	1	1	0	2.2–3.3	
0	1	0	0	1	0	1	1	0	0	0	1	1	?	0	0	0	1	0	0	0	1	1	0	2–3	
0	1	0	0	1	0	1	1	0	0	0	1	1	?	0	0	0	1	0	0	0	1	1	0	1.5–3.5	
0	1	1	2	1	1	1	2	0	1	0	0	0	2	0	1	0	1	1	2	1	1	0	0	2.1–5.1	
0	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	4–6
0	1	1	2	1	1	1	2	0	1	0,1	0	0	0	0	0	0	1	1	2	1	1	0	0	1.8–9.5	
0	1	1	2	1	1	1	2	0	1	0,1	0	0	0	0	0	0	1	1	2	1	1	0	0	1.8–9.5	
0	1	1	2	1	1	1	2	0	1	1	0	0	01	0	0	0	1	1	2	?	1	?	?	2.5–4.7	
0	1	1	2	1	1	1	2	0	1	0	0	0	0	0	1	0	1	1	2	1	1	0	0	0.7–3	
0	1	1	2	1	1	1	2	0	1	0	1	0	0	0	1	0	1	1	2	1	1	0	0	1.1–6	
0	1	1	2	1	1	1	2	0	1	0	0	0	0,1	0	1	0	1	0	2	1	1	0	0	0.9–3.3	
0	1	1	2	1	?	?	?	?	?	?	0	0	0	0	0	0	1	1	2	?	?	?	?	1.1–2.2	
0	1	1	2	1	1	1	3	0	1	1	1	0	0	0	0	0	1	1	2	?	1	?	?	11.5–17.5	
0	1	1	2	1	1	1	3	0	1	1	0	0	0,2	0	0	0	1	1	2	1	1	0	0	1.7–12.8	
0	1	1	1	1	1	1	2	0	1	1,2	0	0	0	0	1	0	1	1	1	1	1	0	0	0.8–2.7	
0	1	1	2	1	0	1	2	0	1	1	0	0	0,1	0	1	0	1	1	2	1	1	0	1	1.4–7.7	
0	1	1	1	1	4	1	1	0	1	2	1	0	0	0	1	0	1	1	1	1	1	0	0	0.52–1.2	
0	1	1	2	1	?	?	?	?	?	?	0	0	0,1	0	0	0	1	1	2	?	?	?	?	1.5–3.7	
0	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	3.8–20	
0	1	1	2	1	1	1	2	0	1	1	0	0	0	0	0	0	1	1	2	?	1	?	?	14–20.5	
0	1	1	2	1	1	1	2	0	1	0	1	0	0	0	1	0	1	0	2	1	1	0	0	0.6–3	
0	1	1	2	1	?	?	?	?	?	?	1	0	1,2	0	0	0	1	1	2	?	1	?	?	3.7–7.3	
0	1	1	2	1	1	1	2	0	1	1	1	0	0,1	0	1	0	1	1	1	1	1	0	1	0.6–4.1	
0	1	?	2	?	?	?	?	?	?	?	0	0	1	0	0	0	1	1	2	?	?	?	?	0.6–1.0	
0	1	1	2	1	1	1	2	0	1	0,1	0	0	0	0	0	0	1	1	2	1	1	0	0	2.2–17.2	
0	1	1	2	1	1	1	2	0	1	1	1	0	0	0	1	0	1	1	2	1	1	0	0	0.7–5.8	
0	1	1	2	1	3	1	2	0	1	1	1	0	0	0	0	0	1	1	2	1	1	?	?	7.0–13.0	
0	1	1	2	1	3	1	2	0	1	1	0	0	0	0	0	0	1	0	2	?	1	?	?	7.7–25.0	
0	1	1	2	1	1	1	3	0	1	1	0	0	0,2	0	0	0	1	0	2	1	1	?	?	2.6–10.1	
0	1	1	2	1	1	1	2	0	1	1	0	0	1	0	0	0	1	1	2	1	1	0	0	6.5–26.0	
0	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0	0	1	1	2	1	1	0	0	1.0–6.5	
0	1	0	0	1	0	1	1	0	1	1	1	0	2	0	1	0	1	0	0	1	1	0	1	0.650–2.5	
0	1	0	0	1	1	1	0	0	0	0,2	1	0	?	0	?	0	1	?	0	1	1	0	1	0.650–3.4	
0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	?	0	1	0	0	1	1	0	0	0.6–1.5	
0	1	0	0	1	1	1	0	0	0	1	1	0	0	0	?	0	1	0	0	1	1	0	1	0.350–2.6	
0	1	0	0	1	?	?	?	?	?	?	1	0	0,1	0	?	0	1	0	0	1	1	0	1	0.280–0.9	
0	1	0	0	1	1	1	1	0	0	1	1	0	1,2	0	?	0	1	0	0	1	1	0	1	0.6–2.5	

amounts of homoplasy in the morphological data. Still, several clades, e.g., the genera *Glochidion*, *Breynia/Sauropus*, *Breynia* sect. *Breynia* all have quite a number of apomorphies, which in combination are unique for every entity, making recognition possible.

DISCUSSION

Phylogenetic importance of the morphological characters

Van Welzen (2003), who only used morphology for his phylogenetic analysis of *Sauropus*, found a largely unresolved strict consensus cladogram with mainly autapomorphic qualitative characters. Our results partly confirm Van Welzen’s results. Fig. 3 shows a high amount of (usually homoplasious) autapomorphies. On the other hand, from this MCC tree (Fig. 3) it is also obvious that the morphology makes more sense in

combination with molecular data. Now many internal apomorphies are also present, though most of them show homoplasy. However, it is obvious that combinations of morphological characters are typical for clades. Typical for the clade *Sa. garrettii-Sa. androgynus2* are the large leaves and the papery leaf blades. Both characters are not unique. Papery leaf blades are also found in some *Sauropus* species of Group B1, while large leaves occur in *Glochidion* and *Sa. hirsutus* Beille, but in these taxa both characters never occur in the same combination. Note that only the character optimisations on the well-supported nodes are trustworthy. Most internal nodes within Group A and B1 generally have very low support (most PP below 0.5). Therefore, we will concentrate on the apomorphies of the well-supported nodes for taxon recognition.

The quantitative characters presented some problems. First we used them as continuous characters in TNT, whereby every

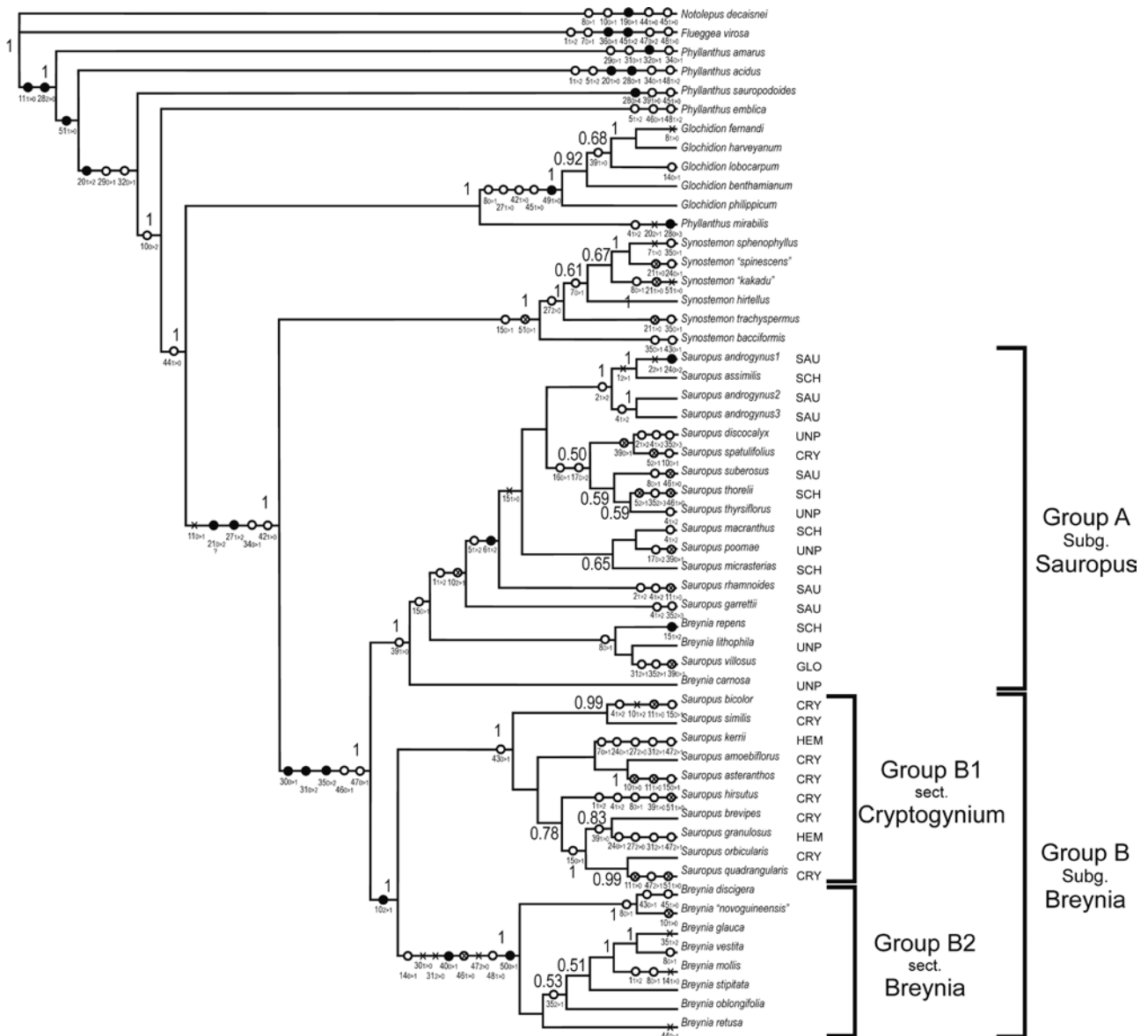


Fig. 3 Character state transformations mapped onto one of the MCC trees of the Bayesian phylogenetic analysis of combined morphological and molecular characters (for latter see Pruesapan et al. 2012). Closed circles are non-homoplasious apomorphies, open circles are parallel developments, crosses are reversals and crosses in open circles parallel reversals. State changes are indicated next to the character number. Above the branches posterior probabilities above 0.5. Absent are the characters 3, 9, 12, 13, 18, 25, 26, 33, 37, 38, 41 (see results), while characters 1 and 4 are depicted in Fig. 4, and characters 21–23, 27, 31, and 47 can be found in Fig. 5. The acronyms indicate former sections: CRY = *Sa.* sect. *Cryptogynium*, GLO = *Sa.* sect. *Glochidioidei*, HEM = *Sa.* sect. *Hemisauropus*, SAU = *Sa.* sect. *Sauropus*, SCH = *Sa.* sect. *Schizanthi*, UNP = unplaced. Clade abbreviations after Pruesapan et al. (2012; Fig. 1).

(slightly) different measurement counted as a different character state and, therefore, the link between evolutionary steps and states became obscure. Also, we disagreed with the automatic a-priori ordering of all quantitative characters in TNT and the use of a mean range from which the (partial) steps were measured relative to the difference between states and the mean values. Therefore, we continued only with the quantitative characters that showed some kind of gap in the measurements (Appendix 2, 3: characters 1–6). Only character 1 (leaf length) is still shown with all original ranges in Fig. 4.

The first chronogram for *Phyllanthaceae* (Luo et al. 2011) used pollen to anchor the crown of *Phyllanthus* s.lat. including *Breynia*, *Sauropus*, and *Glochidion* at 55 Mya; no *Synostemon* species were included in that analysis. Current studies, focused on *Synostemon* (Telford et al. unpubl. data), will address further biogeographic questions in the tribe. Also, a calibrated historical biogeography of *Breynia* s.lat. (including *Sauropus*) will be subject of future studies.

Delimitation of genera

Breynia, *Glochidion*, *Sauropus*, *Synostemon* can 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 unrecognisable, and it will only transfer the problem of recognising monophyletic groups to infrageneric levels. 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 recognised as distinct genera; of which some are in current use, thus minimising name changes. Other reasons are discussed in Pruesapan et al. (2012). Our strategy is to add more to the backbone phylogeny of *Phyllanthus* (Kathriarachchi et al. 2006) in the way of this study. The various clades A–O in Kathriarachchi et al. (2006: f. 2) can serve as a basis (*Breynia*/*Sauropus* form clade M together with *Glochidion* and *Phyllanthus* subg. *Phyllanthodendron*). Forty-two genus names, synonymised with *Phyllanthus* (Webster 1994, Radcliffe-Smith 2001), are already available for the various monophyletic clades in *Phyllanthus*.

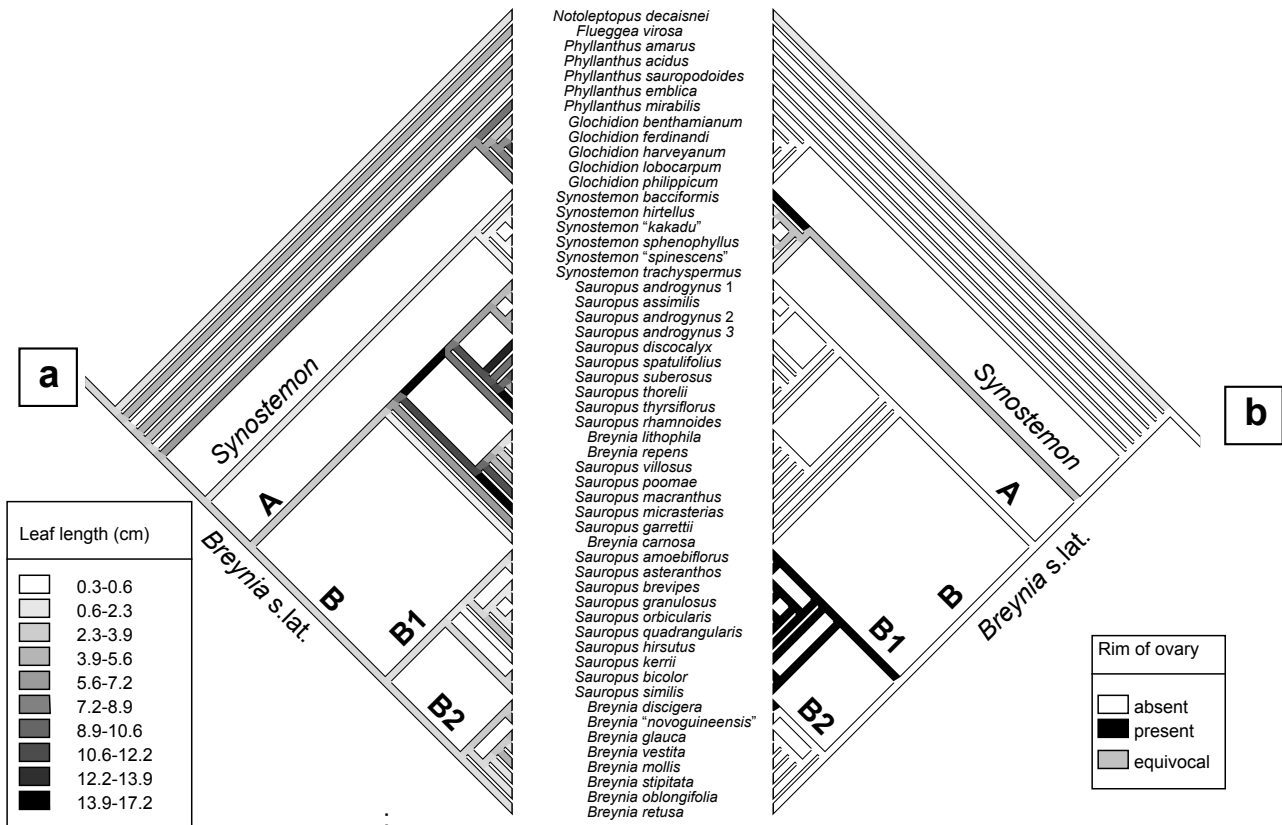


Fig. 4 The MCC tree of Fig. 3 with character state transformations of: a. leaf size (character 1 and 52, latter with many states to show variation) and b. presence of a rim at the edge of the ovary (character 43). Clade A shows the species of *Breynia* subg. *Sauropus*. Clade B shows the species of *Breynia* subg. *Breynia*; comprised of clade B1 presenting the species of sect. *Cryptogynium* and clade B2 presenting the species of sect. *Breynia*.

The paraphyly of *Sauropus* can be solved in three ways (see Fig. 3): 1) *Sauropus* (Group A and Group B1) and *Breynia* (Group B2) could be united under *Breynia*; or 2) only Group B with two sections of *Sauropus* (Group B1) and *Breynia* (Group B2) may be united as *Breynia* (thus restricting *Sauropus* to Group A); or 3) Group A, B1 and B2 all receive generic recognition. The last option will leave *Breynia* as it is, but will split *Sauropus* into two groups that are difficult to recognise (see below), because of the similarities in flower and fruit structure. The second option shows the same problem; the part of *Sauropus* (Group B1) united with *Breynia* cannot easily be distinguished from *Sauropus* Group A. We prefer the first option for two reasons: 1) the molecular reconstructions by Pruesapan et al. (2008, 2012) never showed the clear-cut separation of *Sauropus* species from *Breynia* because of various polytomies; 2) the union of *Sauropus* under *Breynia* will increase the recognisability of *Breynia* s.lat. by emphasizing their morphological unity in flower, fruit, and seed characters, which distinguish them from *Synostemon*.

Several characters form synapomorphies for the broader concept of *Breynia*. The disc glands or sepal scales in the staminate flowers (Fig. 5, illustrated in Fig. 6c–e) are absent in most *Synostemon* species with the exception of *Sy. bacciformis*, which is basal in the *Synostemon* clade, and *Sauropus* (= *Synostemon*) *anemoniflorus* J.T. Hunter & J.J. Bruhl (1997), which was not included in the analysis. Presence of the scales is a likely synapomorphy at the base of Group A+B+*Synostemon*, with a change to absence near the base of the *Synostemon* clade (above *Sy. bacciformis*) and parallel changes to absence in the *Breynia* s.lat. *Hemisauropus* group (represented by *Sa. kerrii* Airy Shaw) and *Sa. granulatus* Airy Shaw (formerly part of the *Hemisauropus* group, but see below). 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. Typical apomorphies for *Breynia* s.lat. are the shape of the fruits, which are wider than high, and the seeds, which are smooth (seed: char. 51; both characters illustrated in Pruesapan et al. 2012: f. 3, B, E, H for fruit, C, F, I for seed). *Synostemon* has fruits that are higher than wide and the seeds are prominently sculptured. The pistillate flowers also show a difference. *Breynia* s.lat. 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 and the stigmas are generally not split or slightly bifid to mostly split less than halfway (characters 45, 46 in Fig. 3; see also Pruesapan et al. 2012: f. 3A, D, G).

Comparing phylogenetic classification with traditional classification

In this discussion we show characters that can be used to distinguish the various groups and which characters were traditionally used. Some sections of *Sauropus* sensu Müller Argoviensis (1863, 1866) and Airy Shaw (1969) are corroborated by our phylogenetic reconstruction (Fig. 3). Species of *Sauropus* sections *Glochidioidei*, *Schizanthi*, and *Sauropus* form Group A (Fig. 1, 3). Added to this group are several unplaced species and the misplaced *Sa. spatulifolius* Beille, which was originally classified in sect. *Cryptogynium* (Fig. 1, 3, Table 2). None of the sections is present as a monophyletic clade, and the cladograms (Fig. 1, 3) show no supported groups within the Group A clade with the exception of the *Sa. androgynus*/*Sa. assimilis* complex. Thus, we unite all species and sections in Group A as *Breynia* subg. *Sauropus*. This group contains the type of *Sauropus* (*Sa. albicans* Blume = *Sa. androgynus*). Group B (Fig. 1, 3) is composed of a clade with *Sauropus* species (Group B1) and one with *Breynia* species (Group B2). Fig. 3 shows high support for the three clades (B, B1, B2). Thus, we

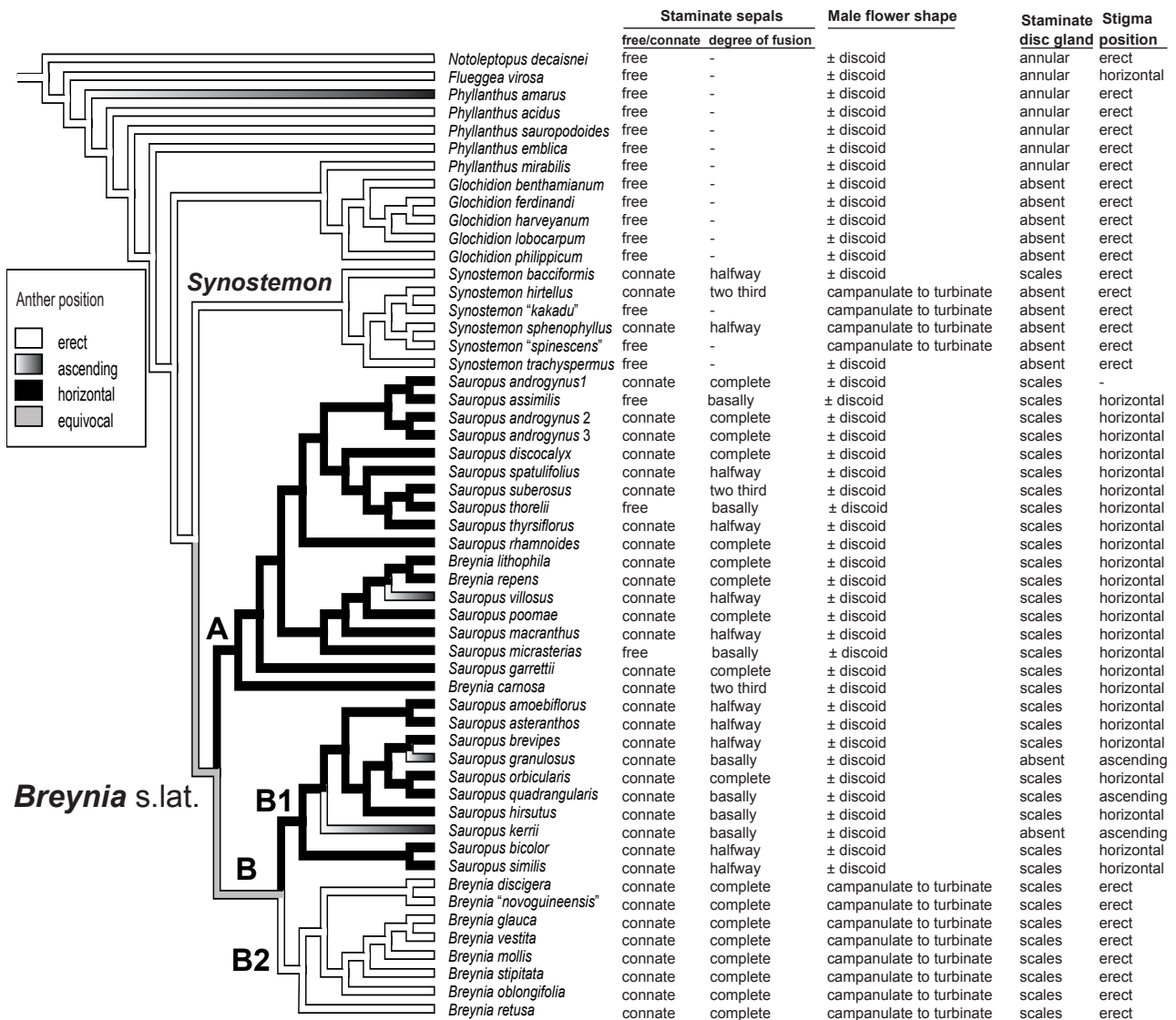


Fig. 5 The MCC tree of Fig. 3 with character state transitions in the anther position (char. 31), connation (char. 21) and degree of fusion (char. 22) of the staminate sepals, staminate flower shape (char. 23), the presence of a disc in the staminate flowers (char. 27), and the stigma position (char. 47). '-' indicates that the character is not applicable. Clade A shows the species of *Breynia* subg. *Sauropus*. Clade B shows the species of *Breynia* subg. *Breynia*; comprised of clade B1 presenting the species of sect. *Cryptogynium* and clade B2 presenting the species of sect. *Breynia*.

unite these species in clade B as *Breynia* subg. *Breynia*. Group B1 (Fig. 3) comprises *Sauropus* sect. *Cryptogynium* (except *Sa. spatulifolius*) and *Sa.* sect. *Hemisauropus*. Both sections have to be combined, because the latter is nested within the former.

Sauropus sect. *Hemisauropus* is underrepresented in the sampling, because we were unable to extract DNA from the thick leaves in this group, probably a result of either an abundance of secondary metabolites or decomposed DNA due to relatively slow drying of the thick leaves. *Sauropus kerrii* is representative for this group, the group 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: f. 2d). *Sauropus granulosus*, formerly part of sect. *Hemisauropus*, is separate from this section in the phylogeny (Fig. 3). Our results corroborate relationships derived from pollen data (Sagun & Van der Ham 2003), in which *Sa. granulosus* groups with the main pollen type of *Sauropus*, pollen with a perforate to reticulate ornamentation and subprolate to oblate-spheroidal shape, while *Sa. kerrii* possesses typical *Sa.* sect. *Hemisauropus* pollen with a distinct perforate ornamentation, and prolate-spheroidal to subprolate shape. This means that the *Sa.* sect. *Hemisauropus* group (*Sa. granulosus* excepted) may be a monophyletic group within Group B1. All these taxa

are united in *Breynia* subg. *Breynia* sect. *Cryptogynium* (oldest available name: Müller Argoviensis 1863).

Clade B2 (Fig. 3) contains only species of *Breynia*, which we here recognise as *Breynia* subg. *Breynia* sect. *Breynia*. The type of *Breynia*, *B. disticha*, was not included as our sample did not yield DNA; the species had been included in the *matK* and ITS analyses of Kathriarachchi et al. (2006) and Pruesapan et al. (2008). In those analyses, *B. disticha* was a member of a strongly supported clade with the other samples of *Breynia*. One species of former *Melanthesopsis* Müll.Arg. was included here, *B. retusa* (Dennst.) Alston, and although it appeared as sister to the remaining taxa of *Breynia* s.str. (Group B2; Fig. 3), it is clearly part of Group B2. Therefore, synonymy of *Melanthesopsis*, as discussed in the introduction, is supported.

Morphological recognition of new groups

The characters useful for the recognition of *Breynia* (including *Sauropus*) and infrageneric groups are discussed here. The character optimisation, where possible, can be found in Fig. 3 and special characters are highlighted in Fig. 4 and 5.

Pax & Hoffmann (1922) grouped all species with large leaves, longer than 4 cm, into *Sa.* sect. *Sauropus* and *Sa.* sect. *Schi-*

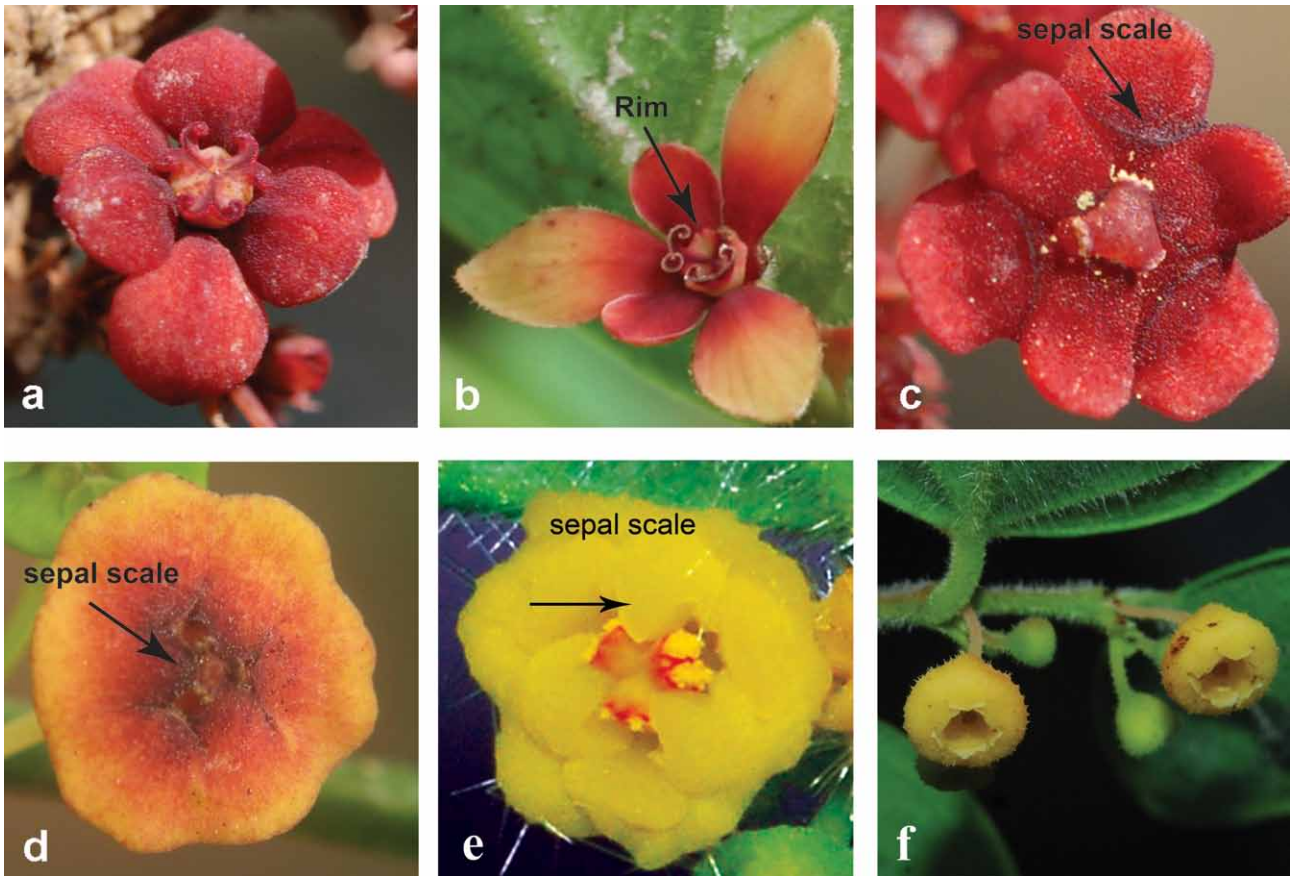


Fig. 6 a, b: Pistillate flowers with horizontal stigmas and absence (a) or presence (b) of a rim at the edge of the ovary; c–f: staminate flowers with horizontal anthers (c, d) and ascending anthers (e); sepals scales indistinct (c) and lobed (d, e); calyx with a dissected (c) or hardly lobed (d, e) and completely connate sepals (f); a, c: *Sa. spatulifolius* Beille; b: *Sa. hirsutus* Beille; d: *Sa. androgynus* (L.) Merr.; e: *Sa. villosus* (Blanco) Merr.; f: *B. stipitata* Müll.Arg. — Photo's by: a, c, e. Kanchana Pruesapan; b. Bhanumas Chantarasuwan; d. Siriporn Zungsonthiporn.

zanthi. *Sauropus* sect. *Glochidioidei*, proposed by Airy Shaw (1969), also shares this character. Larger leaf size is a synapomorphy for Group A, *Breynia* subg. *Sauropus* minus *B. carnosa* Welzen & Pruesapan (Fig. 4a); *B. carnosa* is still a small-leaved species basal in clade A. Leaves up to 3.9 cm are characteristic of Group B, *B.* subg. *Breynia* (Fig. 4a).

Sauropus spatulifolius has always been classified in *Sa.* sect. *Cryptogynium* (e.g., Airy Shaw 1969; Table 2), but in our previous and present analyses (Pruesapan et al. 2008, 2012) it is part of Group A (Fig. 1, 3–5). Its placement in this clade is corroborated by its possession of larger leaves (Fig. 4a), indicating the taxonomic utility of this character in the study group.

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' values in some species, not continuous ranges within species. For example, in *Sa.* sect. *Hemisauropus* (placed by molecular evidence in the small-leaved Group B1, see above) there are a few species, not sampled here, i.e., *Sa. rostratus* Miq. (will become *Breynia temii* (Welzen & Chayam.) Welzen & Pruesapan, see below), *Sa. shawii* Welzen and *Sa. subterblancus* (C.E.C.Fisch.) Welzen, which have leaves up to 7, 11.2 and 7.5 cm long, respectively. Three new species (already described under *Breynia*, but part of subg. *Sauropus*; Van Welzen & Pruesapan 2010), *B. carnosa*, *B. lithophila* Welzen & Pruesapan, and *B. repens* Welzen & Pruesapan 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 Group A.

Several members of the 'larger-leaved' group A have compound inflorescences (even up to 60 cm long!) rather than simple axil-

lary fascicles, which are always found in the small-leaved Group B1 (including the larger-leaved species of sect. *Hemisauropus*) and Group B2 (*Breynia* s.str.). However, Van Welzen (2003) already showed that these compound inflorescences are 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 apically). The different types of compound inflorescences (char. 17, state 2) are autapomorphies for *Sa. micrasterias* Airy Shaw and *Sa. poomae* Welzen and a synapomorphy for *Sa. discocalyx-thyrsoiflorus*, though among the latter the inflorescences differ enormously. A compound inflorescence is certainly not a synapomorphy for Group A as suggested by a reviewer.

In general, especially in subg. *Sauropus*, the top of the ovary is flat, but the margin can show an upright rim or not (Fig. 4b, 6a, b). Group A (Fig. 4b, 6a) has ovaries without a rim, and again, the placement of *Sa. spatulifolius* in this clade agrees well, because this species also lacks an ovary rim (Fig. 6a). The species in Group B1 (Fig. 4b) have ovaries with a lateral rim (Fig. 6b), at least between the stigmas. Within Group B2 the situation is somewhat more complex, with most species showing no rim and only few species 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). Van Welzen (2003) reported that most species of *Sauropus* have horizontal stigmas (Fig. 5, 6a, b), while erect stigmas evolved independently in Group B1 in *Sa. quadrangularis* (Willd.) Müll.Arg. (Van Welzen 2003: f. 5c), a member of sect. *Cryptogynium*, the species of sect. *Hemisauropus* (Van Welzen 2003: f. 3d), and most species of *Breynia* (except *B. retusa*).

The shape of the staminate calyx is discoid with almost free to completely fused sepals in *Sauropus* (Fig. 5, 6c–e) and campanulate-turbinate with fused sepals in *Breynia* (Fig. 5, 6f). However, *Sa. granulatus* and the *Hemisauropus* group (represented by *Sa. kerrii*) have free sepals of which the apices are generally infolded, certainly of three of the sepals, whereby the inner apical part becomes connate with the basal part of the sepal.

The androecium shows three types (Fig. 5, 6c–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. 6c, d). In *Sa. kerrii* and *Sa. granulatus* the anthers are much larger and semi-erect like in *Sa. villosus* (Blanco) Merr. (Fig. 6e). *Breynia* has a completely different type; the androecium forms a sturdy androphore with the anthers vertically and longitudinally along the upper part (Fig. 6f). The changes in the androecium and the shape of the staminate flower between *Sauropus* and *Breynia* is probably the result of the pollination mutualism between *Breynia* and *Epicephala* moths (Kawakita & Kato 2009, and references therein). This seemingly induced changes in the staminate flower, making it more or less exclusively accessible for the moths to actively gather pollen, as well as in the pistillate flowers by reduction of the stigmas. Because of these differences in morphology *Sauropus* and *Breynia* were always kept separate. The *Epicephala* pollination originated several times independently in the *Phyllanthaceae* (Kawakita & Kato 2009).

The degree of connation of the staminate sepals is extremely variable (Fig. 5), but was used by Pax & Hoffmann (1922) to distinguish some sections in *Sauropus*. The species with (almost) completely connate sepals (Fig. 6d, e) were mainly placed in subg. (*Holo*)*Sauropus* by Pax & Hoffmann. Two of these species, *Sa. androgynus* and *Sa. rhamnoides* Blume, have an almost similar widespread distribution (Van Welzen 2003), ranging from India to East Malesia, and are difficult to distinguish (apex of leaves different, gradually tapering in *Sa. androgynus*, convex at both sides in *Sa. rhamnoides*). However, the phylogeny shows that they are not closely related (Fig. 3). Most species with completely connate sepals appear in Group A (Fig. 5), but not as a distinct group, which means that sect. *Sauropus* as defined by Pax & Hoffmann (1922) cannot be maintained. Moreover, the same condition of completely connate sepals also independently appeared once in Group B1 (*Sa. orbicularis* Craib). Pax & Hoffmann (1922) placed the species with almost free sepals (basally connate) in sect. *Schizanthi* (Van Welzen 2003: f. 2b). However, the four species representing this section in the cladogram (Fig. 3: *Sa. assimilis* Thwaites, *Sa. macranthus* Hassk., *Sa. micrasterias* and *Sa. thorelii* Beille), originated independently and for this reason this section cannot be maintained either. The (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*.

***Sauropus androgynus* complex**

Sauropus assimilis, and three samples of *Sa. androgynus* form a strongly supported clade (Fig. 3–5, support in Fig. 3). Originally, these species were placed in *Sa. sect. (Eu)Sauropus* (Müller Argoviensis 1863, 1866, Hooker 1887). Later *Sa. assimilis* was placed into *Sa. sect. Schizanthi* (Pax & Hoffmann 1922; Table 2) based on having almost free staminate sepals. *Sauropus androgynus* 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, which is generally completely connate and

rather round and varies between 2.5–20 mm diam (Fig. 6d). The very large calyx varies from flat (typical *Sa. androgynus*) to recurved (former *Sa. retroversus* Wight). 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 *Sa. assimilis*, which typically has free staminate sepal lobes. Free staminate sepal lobes are incidentally found throughout the range of *Sa. androgynus*. All three forms have the *Sa. androgynus* type of leaf. Van Welzen (2003) placed *Sa. retroversus* in synonymy under *Sa. androgynus*. Analyses of nuclear (Pruesapan et al. 2012) and chloroplast (Pruesapan et al. 2008) data found former *Sa. retroversus* and *Sa. assimilis* to be sister species, and both in turn sister to typical *Sa. androgynus*. By contrast Kathriarachchi et al. (2006) found no support for a close relationship between former *Sa. retroversus* and *Sa. androgynus* and thus argued that former *Sa. retroversus* is not a synonym of *Sa. androgynus*. 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 *Sa. androgynus* and *Sa. retroversus*. The two herbarium specimens available from Sri Lanka of *Sa. assimilis* appear to be an exceptional form of *Sa. androgynus*, with a deeply divided calyx, and it should be also considered as conspecific with *Sa. androgynus*. Based on our extensive study of herbarium material, together with morphological and molecular analysis, we here (see below) place *Sa. assimilis* as synonym under *Sa. androgynus*.

CONCLUSIONS

Our study provides additional morphological arguments for the union of *Sauropus* with *Breynia* under the latter, older name (Pruesapan et al. 2012). The new circumscription of *Breynia* is monophyletic and morphologically typical characters are the broader than high fruits, smooth seeds, and flowers with usually scales in the staminate flowers. Our molecular phylogeny recovers three groups, which we recognise as taxa within *Breynia*. We recognise *Breynia* subg. *Sauropus*, and *Breynia* subg. *Breynia*. Sections *Cryptogynium* and *Breynia* can be recognised within *B. subg. Breynia*. All groups have their typical characters. *Breynia* subg. *Sauropus* generally has larger leaves, horizontal anthers, and lacks a marginal rim on top of the flattened ovary; *Breynia* subg. *Breynia* has smaller leaves, horizontal to ascending to vertical stamens, and the stigmas, especially of the former species of *Sauropus*, have a rim. *Breynia* sect. *Cryptogynium* is characterised by horizontal to ascending anthers and an ovary with a rim, and sect. *Breynia* with vertical anthers and the ovary normally without a rim. This classification is formalised below.

TAXONOMY

Here we transfer the species of *Sauropus* to *Breynia*. Most synonyms of *Sauropus* names are not repeated here, but can be found in Van Welzen (2003). Chakrabarty & Balakrishnan (2009) followed Hoffmann et al. (2006) and transferred the names of the Indian species of *Breynia*, *Glochidion*, and *Sauropus* to *Phyllanthus*. Recently, based on our studies (Pruesapan et al. 2008) Chakrabarty & Balakrishnan (2012) transferred a number of *Sauropus* names to *Breynia*, something we intended to do more elaborately here. Unfortunately, one of their new combinations, *B. bacciformis*, pertains to a *Synostemon* species. *Synostemon* is reinstated as a genus, and therefore the name given under *Breynia* by Chakrabarty & Balakrishnan (2012) is synonymised here with the accepted *Synostemon* name.

Synostemon F.Muell.

Synostemon F.Muell. (1859) 32. — Lectotype (designated by Wheeler 1975: 537): *Sy. ramosissimus* F.Muell.

Note — The genus is currently under revision by Telford. Several new species have been recognised from morphological studies and several have been tested using molecular phylogenetics (Pruesapan et al. 2012); two of these new species are included in Fig. 2–5.

Synostemon bacciformis (L.) G.L.Webster

Synostemon bacciformis (L.) G.L.Webster (1960) 26, in adnot. — *Phyllanthus bacciformis* L. (1767b) 294. — *Agyneia bacciformis* (L.) A.Juss. (1824) 24, t. 6. — *Agyneia phyllanthoides* Spreng. (1826) 19, nom. illeg., nom. superfl. — *Diplomorpha bacciformis* (L.) Kuntze (1891) 603. — *Sauropus bacciformis* (L.) Airy Shaw (1980a) 221. — *Breynia bacciformis* (L.) Chakrab. & N.P.Balakr. (2012) 120. — Lectotype (designated by Scott in Bosser et al. 1982: 37): *Koenig s.n.* = *Herb. Linn 1105.6* (LINN), Sri Lanka.

Note — For heterotypic synonyms see Van Welzen (2003) under *Sa. bacciformis*.

The combination *Synostemon trachyspermus* (F.Muell.) Airy Shaw (1981b) is invalid as the basionym lacked its literature reference. The opportunity is taken here to validate the combination:

Synostemon trachyspermus (F.Muell.) I. Telford & Pruesapan, *comb. nov.*

Phyllanthus trachyspermus F.Muell., *Fragm.* 1 (1855) 14. — *Diasperus trachyspermus* (F.Muell.) Kuntze (1891) 601. — *Glochidion trachyspermum* (F.Muell.) H.Eichler (1965) 210. — *Sauropus trachyspermus* (F.Muell.) Airy Shaw (1980b) 685. — Type: *F. (von) Mueller s.n.* (holotype MEL), Australia, 'on places subject to inundations at the junction of the rivers Darling and Murray'.

Note — Morphological studies (Telford et al. unpubl.) find *Sa. trachyspermus*, as treated by Hunter & Bruhl (1997), to be an heterogeneous species assemblage.

Breynia J.R. Forst. & G.Forst.

Breynia J.R. Forst. & G.Forst. (1775) 73, nom. cons. (non *Breynia* L., 1753: 503, nom. rej., *Capparaceae*). — Type: *Breynia disticha* J.R.Forst. & G.Forst. *Melanthesa* Blume (1826) 590. — Lectotype (designated by Webster 1994: 46): *Melanthesa racemosa* Blume (= *Breynia racemosa* (Blume) Müll.Arg.). *Melanthesopsis* Müll.Arg. (1863) 74; (1866) 436. — Lectotype (designated by Wheeler 1975: 537): *Melanthesopsis lucens* (Poir.) Müll.Arg. (= *Breynia fruticosa* (L.) Hook.f.).

Breynia sect. Breynia

Breynia J.R.Forst. & G.Forst. sect. *Breynia*: Literature and type as under the genus.

Breynia sect. *Breyniastrum* Baill. (1866) 344. — Lectotype (designated here by Esser): *Breynia stipitata* Müll.Arg.

All species of *Breynia* s.str. (*Breynia* in the old sense) belong in this type section. These need no new combinations, and the Malesian species are still under revision by Esser & Stuppy. A checklist of accepted names under *Breynia* in the old sense can be found in Govaerts et al. (2000a: 278–284). Only the two new combinations under *Phyllanthus* of Chakrabarty & Balakrishnan (2009) have to be synonymised with the original names in *Breynia*.

Breynia racemosa (Blume) Müll.Arg.

Breynia racemosa (Blume) Müll.Arg. (1866) 441. — *Melanthesa racemosa* Blume (1826) 492. — *Phyllanthus racemifer* Steud. (1841) 327, nom.

nov. — *Phyllanthus racemosus* (Blume) Chakrab. & N.P.Balakr. (2009) 712. — Lectotype (designated here by Esser): *Blume 1036* (lectotype L, sheet no. 903.155-99; isolectotypes A, L), (Indonesia), Java, 'prope Parong provinciae Buitenzorg'.

Breynia vitis-idaea (Burm.f.) C.E.C.Fisch.

Breynia vitis-idaea (Burm.f.) C.E.C.Fisch. (1932) 65. — *Rhamnus vitis-idaea* Burm.f. (1768) 61, p.p., only lectotype. — *Phyllanthus rhamnoides* Retz. (1788) 30, nom. illeg., nom. superfl. — *Phyllanthus vitis-idaea* (Burm.f.) Chakrab. & N.P.Balakr. (2009) 712. — Lectotype (designated by Radcliffe-Smith 1986: 14): *Breynia*, *Exot. Pl. Cent.*: 8, t. 4. 1678.

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

Sauropus Blume sect. *Cryptogynium* Müll.Arg., *Linnaea* 32 (1863) 73; (1866) 243, as '*Ceratogynium*'; Hook.f. (1887) 334, as '*Ceratogynium*'; Pax & K.Hoffm. (1922) 222, as '*Ceratogynium*'; Airy Shaw (1969) 43. — Type: *Sauropus rigidus* Thwaites (= *Breynia quadrangularis* (Willd.) Welzen & Pruesapan) (referred originally to Wight's genus name *Cryptogynium*, but as the oldest available name in its rank is - erroneously *Cryptogynium*, it must be maintained; see Airy Shaw 1969).

Ceratogynium Wight (1852) 26. — Type: *Ceratogynium rhamnoides* Wight (= *Breynia quadrangularis* (Willd.) Welzen & Pruesapan).

Sauropus Blume sect. *Hemisauropus* Müll.Arg. (1866) 243; Airy Shaw (1969) 55. — *Sauropus* Blume subg. *Hemisauropus* (Müll.Arg.) Pax & K.Hoffm. (1922) 225. — Type: *Sauropus rostratus* Miq. (= *Breynia temii* (Welzen & Chayam.) Welzen & Pruesapan).

Breyniopsis Beille (1925) 157; (1927) 630. — Type: *Breyniopsis pierreii* Beille (= *Breynia pierreii* (Beille) Welzen & Pruesapan).

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

Sauropus amoebiflorus Airy Shaw, *Kew Bull.* 23 (1969) 45. — Type: *Kerr 9023* (holotype K; isotypes BM, L, P), Thailand (Siam), South-western, Ratchaburi Prov., Ratchaburi (Ratburi).

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

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

Breynia bicolor (Craib) Chakrab. & N.P.Balakr.

Breynia bicolor (Craib) Chakrab. & N.P.Balakr. (2012) 120. — *Sauropus rigidus* Craib (1911) 457, nom. inval., non Thwaites (1864). — *Sauropus bicolor* Craib (1914a) 11. — *Phyllanthus thailandicus* Chakrab. & N.P.Balakr. (2009) 715, non *P. bicolor* Vis., nor Müll.Arg. — Lectotype (designated by Van Welzen 2003: 347): *Kerr 651* (K; isolectotypes A, BM, K), Thailand (Siam), Northern, Chiang Mai Prov., Doi Sutep.

Note — For heterotypic synonyms see Van Welzen (2003). Here synonym under *Phyllanthus* added.

Breynia brevipes (Müll.Arg.) Chakrab. & N.P.Balakr.

Breynia brevipes (Müll.Arg.) Chakrab. & N.P.Balakr. (2012) 121. — *Sauropus brevipes* Müll.Arg. (1863) 73. — *Aalius brevipes* (Müll.Arg.) Kuntze (1891) 591. — *Phyllanthus myanmarensis* Chakrab. & N.P.Balakr. (2009) 715, non *P. brevipes* Hook.f. — Type: *Wallich 28* (holotype G-DC, 2 sheets, IDC microfiche DC herbarium 2461/12, 13), India, Prome.

Note — For heterotypic synonyms see Van Welzen (2003). Here the new combination under *Phyllanthus* is added as a synonym.

Breynia delavayi (Croizat) Welzen & Pruesapan, *comb. nov.*

Sauropus delavayi Croizat, *J. Arnold Arbor.* 21 (1940) 496. — Type: *Delavay 2845* (holotype A; isotypes A, P), China, Yunnan.

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

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

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

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

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

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

Breynia hirsuta (Beille) Welzen & Pruesapan, *comb. nov.*

Sauropus hirsutus Beille in Lecomte, Fl. Indo-Chine 5 (1927) 657. — Lectotype (designated by Van Welzen 2003: 356): *Pierre 564* (P), Cambodia, Samrong-tong.

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

Sauropus kerrii Airy Shaw, Kew Bull. 23 (1969) 52. — Type: *Kerr 21541* (holotype K; isotypes BK, BM, L, P), Thailand (Siam), Eastern (Ubon Circle), Ubon Ratchathani Prov., Chiet.

Breynia orbicularis (Craib) Welzen & Pruesapan, *comb. nov.*

Sauropus orbicularis Craib, Bull. Misc. Inform. Kew (1914b) 284. — Type: *Kerr 2635* (holotype K; isotypes A, BM, CAL, E), Thailand, Chiang Mai Prov., Doi Sutep.

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

Breynia pierrei (Beille) Welzen & Pruesapan, *comb. nov.*

Breyniopsis pierrei Beille, Bull. Soc. Bot. France (1925) 158. — *Sauropus pierrei* (Beille) Croizat (1940) 494. — Syntypes: *Evrard 110* (P), Vietnam, Cochinchine, Prov. Bien-Hoa, Trang-bon; *Pierre 1792* (A, P), Vietnam, Bao Chang; *Poilane 2442* (P), Vietnam, Prov. Bien-Hao, Gia-ray.

Breynia poilanei (Beille) Welzen & Pruesapan, *comb. nov.*

Sauropus poilanei Beille in Lecomte, Fl. Indo-Chine 5 (1927) 653. — Type: *Poilane 5950* (holotype P; isotypes A, P), Vietnam, Annam, prov. Phanrang, Ca-na.

Breynia po-khantii (Chakrab. & M.Gangop.) Chakrab. & N.P.Balacr.

Breynia po-khantii (Chakrab. & M.Gangop.) Chakrab. & N.P.Balacr. (2012) 121. — *Sauropus po-khantii* Chakrab. & M.Gangop. (1996) 531, f. 7. — *Phyllanthus po-khantii* (Chakrab. & M.Gangop.) Chakrab. & N.P.Balacr. (2009) 715. — Type: *Maung Po Khant 13451* (holotype CAL n.v.), Myanmar (Burma), Tenasserim, Mergui dist., Chaegleya.

Note — The drawing in Chakrabarty & Gangopadhyay (1996: f. 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. Here the new combination under *Phyllanthus* is added as a synonym.

Breynia pulchella (Airy Shaw) Welzen & Pruesapan, *comb. nov.*

Sauropus pulchellus Airy Shaw, Kew Bull. 23 (1969) 54. — Type: *Kerr 20472* (holotype K; isotype BK, BM), Thailand (Siam), Eastern Rachasima Circle, Nakhon Ratchasima Prov. (Korat), Ta Chang.

Breynia quadrangularis (Willd.) Chakrab. & N.P.Balacr.

Breynia quadrangularis (Willd.) Chakrab. & N.P.Balacr. (2012) 121. — *Phyllanthus quadrangularis* Willd. (1805) 585. — *Sauropus quadrangularis* (Willd.) Müll.Arg. (1863) 73. — *Aalius quadrangularis* (Willd.) Kuntze (1891) 591. — Type: *Hb. Willdenow 17985* (holotype B-W; IDC microfiche 7440!), India.

Sauropus rigidus Thwaites (1864) 284. — *Phyllanthus neo-rigidus* Chakrab. & N.P.Balacr. (2009) 715, non *P. rigidus* Tate. — *Breynia rigida* (Thwaites) Chakrab. & N.P.Balacr. (2012) 121. — Type: *Thwaites CP 2135* (holotype K; isotypes BM, CAL n.v., G, PDA n.v.), Sri Lanka (Ceylon).

Sauropus compressus Müll.Arg. (1866) 243. — *Aalius compressus* (Müll.Arg.) Kuntze (1891) 591, as '*compressa*'. — *Sauropus quadrangularis* (Willd.) Müll.Arg. var. *compressus* (Müll.Arg.) Airy Shaw (1972) 337. — *Phyllanthus indo-myanmarensis* Chakrab. & N.P.Balacr. (2009) 715, non *P. compressus* Müll.Arg. — *Breynia compressa* (Müll.Arg.) Chakrab. & N.P.Balacr. (2012) 120. — Syntypes: *Hooker s.n.*, s.d. (G-DC n.v., IDC microfiche DC herbarium 2489/5, K (2 sheets)), India, Sikkim, Regio Trop. — *Sauropus quadrangularis* (Willd.) Müll.Arg. var. *puberulus* Kurz (1877) 350. — *Phyllanthus indo-myanmarensis* Chakrab. & N.P.Balacr. var. *puberulus* (Kurz) Chakrab. & N.P.Balacr. (2009) 715. — *Breynia compressa* (Müll.Arg.) Chakrab. & N.P.Balacr. var. *puberulus* (Kurz) Chakrab. & N.P.Balacr. (2012) 120. — Type: *Kurz 1586* (holotype CAL n.v.), Myanmar.

Note — For more heterotypic synonyms see Van Welzen (2003). Some of the new combinations of Chakrabarty & Bala-krishnan (2012) are synonymised here.

Breynia shawii (Welzen) Welzen & Pruesapan, *comb. nov.*

Sauropus shawii Welzen, Blumea 48 (2003) 372, map 4. — Type: *P.F. Stevens et al. 513* (holotype L; isotypes A, KEP), Malaysia, Sabah, Lahad Datu, Ulu Sungei Segamat.

Breynia similis (Craib) Welzen & Pruesapan, *comb. nov.*

Sauropus similis Craib, Bull. Misc. Inform. Kew (1911) 457. — Lectotype (designated by Van Welzen 2003: 372): *Kerr 1788* (K; isolectotype BM), Thailand, Chiang Mai, Doi Sutep.

Breynia subterblanca (C.E.C.Fisch.) C.E.C.Fisch.

Breynia subterblanca (C.E.C.Fisch.) C.E.C.Fisch. (1939) 98, as '*subterblancum*'. — *Glochidion subterblancum* C.E.C.Fisch. (1927) 211. — *Sauropus subterblancus* (C.E.C.Fisch.) Welzen (2001) 504. — *Phyllanthus subterblancus* (C.E.C.Fisch.) Chakrab. & N.P.Balacr. (2009) 715. — Type: *C.E. Parkinson 1669* (holotype K; isotype K), Myanmar (Burma), South Tenasserim, Kyein Chaung.

Breynia temii (Welzen & Chayam.) Welzen & Pruesapan, *comb. nov.*, nom. nov., non *B. rostrata* Merr.

Sauropus temii Welzen & Chayam., Kew Bull. 56 (2001) 654. — Type: *Smitinand 2877* (BKF), Thailand, Peninsular, Surat Thani Prov., Bang Bao. *Sauropus rostratus* Miq., Fl. Ned. Ind., Eerste bijv. (1861) 179, 447. — *Aalius rostratus* (Miq.) Kuntze (1891) 591, as '*rostrata*'. — Lectotype (designated by Van Welzen 2003: 370): *Teijsmann HB 3678* (U), Indonesia, Sumatra, Palembang Prov., River Lamatang near Koeripan (Kuripan).

Note — The combination *Breynia rostrata* Merr. is already in use, therefore, the epithet of the next synonym is selected as epithet for the new combination.

Breynia tsiangii (P.T.Li) Welzen & Pruesapan, *comb. nov.*

Sauropus tsiangii P.T.Li, Acta Phytotax. 25 (1987) 135. — Type: *Zhi-Nan Exped. s.n.* (Inst. Bot. Acad. Sin. Herb. 990841) (holotype PE n.v.), China, Guangxi, Longzhou, Shuikou.

Note — Based on the protologue description of the species, it is placed in *Breynia* sect. *Cryptogynium*.

Breynia* subg. *Sauropus* (Blume) Welzen & Pruesapan, *comb. & stat. nov.

Sauropus Blume, Bijdr. 12 (1826) 595. — *Sauropus* sect. *Eusauropus* Müll. Arg. (1863) 72; (1866) 240; Hook.f. (1887) 332, nom. inval., Art. 21.3 (McNeill et al. 2012). — *Sauropus* subg. *Holosauropus* Pax & K.Hoffm. (1922) 216, nom. inval., Art. 22.2. — *Aalius* Rumph. [(1743) 207; ex Lam. (1783) 1, nom. inval., Art. 32.1(d)] ex Kuntze (1891) 590, nom. illeg., nom. superfl. — Lectotype (designated by Webster 1994: 46): *Sauropus albicans* Blume [= *Breynia androgyna* (L.) Welzen & Pruesapan].

Sauropus Blume sect. *Sphaeranthi* Pax & K.Hoffm. (1922) 220. — Type: *Sauropus stipitatus* Hook.f. [= *Breynia gynophora* Welzen & Pruesapan].

Sauropus Blume sect. *Retroversi* Pax & K.Hoffm. (1922) 221. — Type: *Sauropus retroversus* Wight [= *Breynia androgyna* (L.) Welzen & Pruesapan].

Sauropus Blume sect. *Schizanthi* Pax & K.Hoffm. (1922) 221. — Lectotype (designated by Van Welzen 2003: 331): *Sauropus trinervius* Wall. ex Müll. Arg. [= *Breynia trinervia* (Wall. ex Müll. Arg.) Welzen & Pruesapan].

Sauropus Blume sect. *Glochidioidei* Airy Shaw (1969) 51. — 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 (1969) 49. — Type: *Put 4102* (holotype K; isotypes A, BK, BM, L, P), Thailand (Siam), prov. Nakhon Sawan (Nakawn Sawan), Hua Wai.

***Breynia androgyna* (L.) Chakrab. & N.P.Balacr.**

Breynia androgyna (L.) Chakrab. & N.P.Balacr. (2012) 120. — *Clusia androgyna* L. (1767a) 663; (1767b) 128. — *Aalius androgyna* (L.) Kuntze (1891) 591. — *Sauropus androgynus* (L.) Merr. (1903) 30. — *Phyllanthus androgynus* (L.) Chakrab. & N.P.Balacr. (2009) 714. — Lectotype (designated by Van Welzen 2003: 340): *Hb. Linn. 1206.14* (LINN), 'Habitat in India'.

Sauropus retroversus Wight (1853) t. 1951 (left). — *Aalius retroversus* (Wight) Kuntze (1891) 591, as '*retroversa*'. — *Phyllanthus retroversus* (Wight) Chakrab. & N.P.Balacr. (2009) 715. — *Breynia retroversa* (Wight) Chakrab. & N.P.Balacr. (2012) 121. — Syntypes: *Anonymous s.n.* (K), Sri Lanka; *Thwaites CP 3134* (G-DC n.v., K, P), Sri Lanka, Central Prov., Oodoopussalawa; *Walker 274* (K), Sri Lanka.

Sauropus assimilis Thwaites (1861) 284, syn. nov. — *Phyllanthus assimilis* (Thwaites) Chakrab. & N.P.Balacr. (2009) 715. — *Breynia assimilis* (Thwaites) Chakrab. & N.P.Balacr. (2012) 120. — Type: *Thwaites CP 2855* (holotype K), Sri Lanka (Ceylon), Central Prov., Allagalla.

Sauropus convexus J.J.Sm. (1924) 82, syn. nov. — Neotype (designated here): *Hortus Bogoriensis s.n.*, cultivated (L, barcode L0138208), Indonesia, Java, Bogor. 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) and *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 the other heterotypic synonyms see Van Welzen (2003). Some of the new combinations under *Breynia* of Chakrabarty & Balakrishnan (2012) are synonymised here.

Breynia asymmetrica* (Welzen) Welzen & Pruesapan, *comb. nov.

Sauropus asymmetricus Welzen, Blumea 48 (2003) 344. — Type: *Yates 1241* (holotype BM, barcode BM000606476; isotype BM, barcode BM000630941, P), Indonesia, Sumatra.

***Breynia beillei* Welzen & Pruesapan, *comb. nov.*, nom. nov., non *B. racemosa* (Blume) Müll.Arg.**

Sauropus racemosus Beille in Lecomte, Fl. Indo-Chine 5 (1927) 648. — Type: *Balansa 3202* (holotype P; isotype P, 2 sheets), [Vietnam], Tonkin, vallée de Lankok, Mont Bavi.

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

***Breynia bishnupadae* (M.Gangop. & Chakrab.) Chakrab. & N.P.Balacr.**

Breynia bishnupadae (M.Gangop. & Chakrab.) Chakrab. & N.P.Balacr. (2012) 120. — *Sauropus bishnupadae* M.Gangop. & Chakrab. in Chakrab. & M.Gangop. (1996) 524, f. 2A–D. — *Phyllanthus bishnupadae* (M.Gangop. & Chakrab.) Chakrab. & N.P.Balacr. (2009) 715. — Type: *Modder 114* (holotype CAL n.v.), India, Sikkim, Gulma.

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. The combination under *Phyllanthus* is formally added here as synonym.

Breynia bonii* (Beille) Welzen & Pruesapan, *comb. nov.

Sauropus bonii Beille in Lecomte, Fl. Indo-Chine 5 (1927) 651. — Type: *Bon 2873* (holotype P, 3 sheets; isotype A), [Vietnam], Tonkin, Mont Kien-khé.

Breynia discocalyx* (Welzen) Welzen & Pruesapan, *comb. nov.

Sauropus discocalyx Welzen, Blumea 46 (2001) 501, f. 1. — Type: *van Beusekom & Phengkhilai 566* (holotype L; isotypes AAU, BKF, C, E n.v., K, P), Thailand, Peninsular, Khao Saideng, near Ranong.

***Breynia garrettii* (Craib) Chakrab. & N.P.Balacr.**

Breynia garrettii (Craib) Chakrab. & N.P.Balacr. (2012) 120. — *Sauropus garrettii* Craib (1914b) 284. — *Phyllanthus garrettii* (Craib) Chakrab. & N.P.Balacr. (2009) 715. — Type: *Garrett 37* (holotype K; isotype BM, L), Thailand, Doi Inthanon, N by E of the Pah Ngeam.

Note — For synonyms see Van Welzen (2003). The synonym under *Phyllanthus* is added here.

***Breynia gour-maitii* (Chakrab. & M.Gangop.) Chakrab. & N.P.Balacr.**

Breynia gour-maitii (Chakrab. & M.Gangop.) Chakrab. & N.P.Balacr. (2012) 121. — *Sauropus gour-maitii* Chakrab. & M.Gangop. (1996) 529, f. 5A–E. — *Phyllanthus gour-maitii* (Chakrab. & M.Gangop.) Chakrab. & N.P.Balacr. (2009) 715. — Type: *Mohanan 61883* (holotype CAL n.v.), India, Kerala, Trivandrum dist., way to Chamungi.

Note — The drawing in f. 5A–E by Chakrabarty & Gangopadhyay (1996) shows that the species has quite large leaves with the staminate flower typical for species of former sect. *Schizanthi*, included here in subg. *Sauropus*. The combination under *Phyllanthus* is formally added here as synonym.

***Breynia gynophora* Welzen & Pruesapan, *comb. nov.*, nom. nov., non *B. stipitata* Müll.Arg.**

Sauropus stipitatus Hook.f., Fl. Br. India 5 (1887) 333. — *Phyllanthus stipitatus* (Hook.f.) Chakrab. & N.P.Balacr. (2009) 715. — *Breynia stipitata* (Hook.f.) Chakrab. & N.P.Balacr. (2012) 121, nom. illeg., non *B. stipitata* Müll.Arg. — Type: *Griffith s.n.* (holotype K), India, Sikkim, Darjeeling.

Note — The combination *Breynia stipitata* Müll.Arg. already exists. The epithet *gynophora* refers to the stalked ovary and fruit of this species. The combination under *Phyllanthus* is formally added here as synonym.

Breynia kitanovii* (Thin) Welzen & Pruesapan, *comb. nov.

Sauropus kitanovii Thin, Euphorb. Vietnam (1996) 49. — Type: *N.V. Tjep Not-2790* (holotype HNU n.v.), Vietnam, Hoa Binh, Luong Son, Lam Son.

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* subg. *Breynia*.

Breynia lanceolata (Hook.f.) Welzen & Pruesapan, *comb. nov.*, nom. nov., non *B. rhamnoides* (Willd.) Müll.Arg.

Sauropus lanceolatus Hook.f., Fl. Br. India 5 (1887) 333. — Type: *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 *Sa. macrophyllus* Hook.f.), India, East Bengal, Mishmee.

Sauropus rhamnoides Blume, Bijdr. 12 (1826) 596. — *Aalius rhamnoides* (Blume) Kuntze (1891) 591, as '*rhamnoides*'. — *Phyllanthus rhamnifolius* Chakrab. & N.P.Balacr. (2009) 715, non *P. rhamnoides* Retz. — *Breynia macrocalyx* Chakrab. & N.P.Balacr. (2012) 122, nom. illeg., nom. superfl. — Lectotype (designated by Van Welzen 2003: 367): *Blume s.n.* (L, barcode L 0138511), Indonesia, Java, Montis Salak.

Note — The combination *Breynia rhamnoides* (Willd.) Müll. Arg. already exists. Next in line is the epithet *lanceolatus*, which is older than the epithet *macrocalyx* of Chakrabarty & Balakrishnan (2012) and, therefore, it has precedence over the latter superfluous name. For more heterotypic synonyms see Van Welzen (2003).

Breynia macrantha (Hassk.) Chakrab. & N.P.Balacr.

Breynia macrantha (Hassk.) Chakrab. & N.P.Balacr. (2012) 121. — *Sauropus macranthus* Hassk. (1855) 166. — Type: *Teijsmann s.n.* (holotype L, barcode L0138428), Indonesia, Java, Bogor, Hortus Bogoriensis.

Sauropus forcipatus Hook.f. (1887) 334. — *Aalius forcipatus* (Hook.f.) Kuntze (1891) 591, as '*forcipata*'. — *Phyllanthus forcipatus* (Hook.f.) Chakrab. & N.P.Balacr. (2009) 715, non *P. macranthus* Pax, nor *P. spectabilis* Miq. — Type: *Scortechini 1254* (holotype K), Malay Peninsula, Perak.

Note — The combination under *Phyllanthus* is formally added here as synonym; for more synonyms see Van Welzen (2003).

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

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

Note — The species is placed in this subgenus based on the protologue description.

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

Sauropus micrasterias Airy Shaw, Kew Bull. 14 (1960) 354. — Type: *Jacobs 5179* (holotype K; isotype L), Malaysia, Sarawak, 1st Division, rock formation (Bau series) W and E of passage of Sungei Serin (30 miles S of Kuching).

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

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

Breynia repanda (Müll.Arg.) Chakrab. & N.P.Balacr.

Breynia repanda (Müll.Arg.) Chakrab. & N.P.Balacr. (2012) 121. — *Sauropus repandus* Müll.Arg. (1872) 2. — *Phyllanthus repandus* (Müll.Arg.) Chakrab. & N.P.Balacr. (2009) 715. — Type: *T. Anderson 922* (holotype B†), India, prov. Sikkim, Nohore.

Note — The combination under *Phyllanthus* is formally added here as synonym.

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

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

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.) Chakrab. & N.P.Balacr.

Breynia saksenana (Manilal, Prasann. & Sivar.) Chakrab. & N.P.Balacr. (2012) 121. — *Sauropus saksenanus* Manilal, Prasann. & Sivar. (1985) 294, as '*saksenianus*'. — *Phyllanthus saksenanus* (Manilal, Prasann. & Sivar.) Chakrab. & N.P.Balacr. (2009) 715, as '*saksenianus*'. — Type: *Prasanna-kumar SV 10398* (holotype CALI n.v.), India, Kerala, Nilikkal, Silent Valley.

Note — The combination under *Phyllanthus* is formally added here as synonym.

Breynia spatulifolia (Beille) Welzen & Pruesapan, *comb. nov.*

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

Note — The epithet, though unusual, is without an 'h' after the 't', and according to ICN art. 60.1 Ex 1 and 61.1 this is not correctable (McNeill et al. 2012).

Breynia suberosa (Airy Shaw) Welzen & Pruesapan, *comb. nov.*

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

Breynia thoi (Thin) Welzen & Pruesapan, *comb. nov.*

Sauropus thoi Thin, Euphorb. Vietnam (1996) 48. — Type: *Thin, Loc, Binh, Thuoc, Chan NT 1990* (holotype HNU n.v.), Vietnam, Hoa Binh, Luong Son, Lam Son.

Note — The species is placed in this subgenus based on the description.

Breynia thorelii (Beille) Welzen & Pruesapan, *comb. nov.*

Sauropus thorelii Beille in Lecomte, Fl. Indo-Chine 5 (1927) 649. — Type: *Thorel 3227* (holotype P; isotypes K, P, 3 sheets), Laos, Pak-lay, Lakhone.

Breynia thyrsiflora (Welzen) Welzen & Pruesapan, *comb. nov.*

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

Breynia tiepii (Thin) Welzen & Pruesapan, *comb. nov.*

Sauropus tiepii Thin, Euphorb. Vietnam (1996) 49. — Type: *N.V. Tiep Not-2278* (holotype HNU n.v.), Vietnam, Coa Bang, Trung Khanh.

Note — The species is placed in this subgenus based on the description.

Breynia trinervia (Hook.f. & Thomson ex Müll.Arg.) Chakrab. & N.P.Balacr.

Breynia trinervia (Hook.f. & Thomson ex Müll.Arg.) Chakrab. & N.P.Balacr. (2012) 121. — *Sauropus trinervius* Hook.f. & Thomson ex Müll.Arg. (1863) 72. — *Phyllanthus trinervius* (Hook.f. & Thomson ex Müll.Arg.) Chakrab. & N.P.Balacr. (2009) 716. — Syntypes: *J.D. Hooker & T. Thomson s.n.* (G-DC? n.v., K), India, Mts Khasia; *Wallich 7922A* (G-DC? n.v., K, 2 sheets), India, Botanical Garden Calcutta; *Wallich 7922B* (G-DC? n.v., K, 2 sheets), India, Silhet.

Note — The combination under *Phyllanthus* is formally added here as synonym.

***Breynia villosa* (Blanco) Welzen & Pruesapan, comb. nov.**

Kirganelia villosa Blanco, Fl. Filip. (1837) 712. — *Sauropus villosus* (Blanco) Merr. (1934) 86. — Neotype (designated by Van Welzen 2003): *Merrill Species Blancoanae* 931 (holotype L; isotypes A, BM, K, NSW, NY, P, US), Philippines, Luzon, Rizal Prov.

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

***Breynia yanhuiana* (P.T.Li) Welzen & Pruesapan, comb. nov.**

Sauropus yanhuianus P.T.Li, Acta Phytotax. Sin. 25 (1987) 134. — Type: Y.H. Li 12549 (holotype YNTBI, acronym unknown, also not spelled out in protologue, n.v.), China, Yunnan, Cangyuan, Nanla.

Note — The species is placed in this subgenus based on the description.

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.**

Sauropus varieri Sivar. & Balach., J. Econ. Taxon. Bot. 5 (1984) 918. — Type: *Indu AVS 1579* (holotype CAL; isotypes CALI, MH; all n.v.), India, Kerala, Malappuram dist., Kottakkal Arya Vaidya Sala Herbal Garden.

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REFERENCES

- Airy Shaw HK. 1960. Notes on Malaysian Euphorbiaceae. III. A noteworthy new species of *Sauropus* Bl. from Borneo. *Kew Bulletin* 14: 354, 355.
- Airy Shaw HK. 1969. Notes on Malesian and other Asiatic Euphorbiaceae. *Kew Bulletin* 23: 42–55.
- Airy Shaw HK. 1972. The Euphorbiaceae of Siam. *Kew Bulletin* 26: 330–339, 343.
- Airy Shaw HK. 1975. The Euphorbiaceae of Borneo. *Kew Bulletin, Additional Series* 4: 1–245.
- Airy Shaw HK. 1980a. The Euphorbiaceae of New Guinea. *Kew Bulletin, Additional Series* 8: 1–243.
- Airy Shaw HK. 1980b. The Euphorbiaceae (Platylobeae) of Australia. *Kew Bulletin* 35: 669–686.
- Airy Shaw HK. 1981a. The Euphorbiaceae of Sumatra. *Kew Bulletin* 36: 271–272, 342–344.
- Airy Shaw HK. 1981b. *Synostemon*. In: Jessop J (ed), *Flora of Central Australia*: 192–193. Reed Books, Sydney.
- Baillon H. 1866. Euphorbiacées Australiennes. *Adansonia* 6: 282–345.
- Beille L. 1925. Sur quelques Euphorbiacées nouvelles de la flore indochinoise. *Bulletin de la Société Botanique de France* 72: 157–158.
- Beille L. 1927. Euphorbiaceae. In: Lecomte MH (ed), *Flore Générale de l'Indo-Chine* 5: 643–658. Masson & Cie, Paris.
- Blanco M. 1837. *Flora de Filipinas*. Imprenta de Sto. Thomas por D. Candido Lopez, Manila.
- Blume CL. 1826. *Bijdragen tot de Flora van Nederlandsch Indië* 12. Lands Drukkerij, Batavia.
- Bosser J, Cadet T, Guého J, Marais W. 1982. *Flore des Mascareignes, Familles 153–160*. The Sugar Industry Research Institute, Mauritius; Office de la Recherche Scientifique Oure-Mer, Paris; Royal Botanic Gardens, Kew.
- Bremer K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795–803.
- Burman NL. 1768. *Flora Indica*. Cornelius Haak, Leiden; Johannes Schreuder, Amsterdam.
- Chakrabarty T, Balakrishnan NP. 2009. Transfer of Indian species of *Breynia*, *Glochidion* and *Sauropus* to *Phyllanthus* (Phyllanthaceae) – new combinations and new names. *Journal of Economic and Taxonomic Botany* 33: 712–716.
- Chakrabarty T, Balakrishnan NP. 2012. Nineteen new combinations and a new name in *Breynia* J.R.Forst. & G.Forst. (Phyllanthaceae) from Indian subcontinent. *Bangladesh Journal of Plant Taxonomy* 19: 119–122.
- Chakrabarty T, Gangopadhyay M. 1996. The genus *Sauropus* Blume (Euphorbiaceae) in the Indian subcontinent. *Journal of Economic and Taxonomic Botany* 20: 513–545.
- Chantharanothai P. 2007. *Phyllanthus*. In: Van Welzen PC, Chayamarit K (eds), *Flora of Thailand* 8, 2: Euphorbiaceae (genera G–Z): 473–507. The Forest Herbarium, Bangkok.
- Craib WG. 1911. Contributions to the Flora of Siam. *Bulletin of Miscellaneous Information (Kew)*: 457, 458.
- Craib WG. 1914a. Contributions to the Flora of Siam. *Additamenta V. Bulletin of Miscellaneous Information (Kew)*: 11.
- Craib WG. 1914b. Contributions to the Flora of Siam. *Additamenta VII. Bulletin of Miscellaneous Information (Kew)*: 284, 285.
- Croizat L. 1940. New and critical Euphorbiaceae from eastern tropical Asia. *Journal of the Arnold Arboretum* 21: 490–510.
- De Jussieu AHL. 1824. *De Euphorbiacearum Generibus*. Didot fil., Parisii.
- De Queiroz A, Donoghue MJ, Kim J. 1995. Separate versus combined analysis of phylogenetic evidence. *Annual Review of Ecology and Systematics* 26: 657–681.
- Drummond AJ, Rambaut A. 2007. BEAST: Bayesian Evolutionary Analysis by Sampling Trees. *BMC Evolutionary Biology* 7: 214.
- Eichler H. 1965. Supplement to J.M. Black's *Flora of South Australia*, 2nd ed. Government Printer, Adelaide.
- Fischer CEC. 1927. Contributions to the Flora of Burma III. *Bulletin of Miscellaneous Information (Kew)*: 211.
- Fischer CEC. 1932. VII – The Koenig collection in the Lund Herbarium. *Bulletin of Miscellaneous Information (Kew)*: 49–76.
- Fischer CEC. 1939. Contributions to the Flora of Burma XV. *Bulletin of Miscellaneous Information (Kew)*: 98.
- Forster JR, Forster G. 1775. *Characteres Generum Plantarum*, ed. 1. London.
- Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Govaerts R, Frodin DG, Radcliffe-Smith A. 2000a. World checklist and bibliography of Euphorbiaceae (and Pandaceae) 1. Royal Botanic Gardens, Kew.
- Govaerts R, Frodin DG, Radcliffe-Smith A. 2000b. World checklist and bibliography of Euphorbiaceae (and Pandaceae) 4. Royal Botanic Gardens, Kew.
- Hasskarl JK. 1855. *Retzia* 1. Lange & Co., Batavia.
- Hoffmann P, Kathriarachchi H, Wurdack KJ. 2006. A phylogenetic classification of Phyllanthaceae (Malpighiales; Euphorbiaceae sensu lato). *Kew Bulletin* 61: 37–53.
- Hooker JD. 1887. *The Flora of British India* 5. Reeve & Co, London.
- Hunter JT, Bruhl JJ. 1997. New *Sauropus* (Euphorbiaceae: Phyllanthaceae) taxa for the Northern Territory and Western Australia and notes on other *Sauropus* occurring in these regions. *Nuytsia* 11: 165–184.
- Kathriarachchi H, Samuel R, Hoffmann P, Mlinarec J, Wurdack KJ, et al. 2006. Phylogenetics of tribe Phyllanthaceae (Phyllanthaceae; Euphorbiaceae sensu lato) based on nrITS and plastid matK DNA sequence data. *American Journal of Botany* 93: 637–655.
- Kawakita A, Kato M. 2009. Repeated independent evolution of obligate pollination mutualism in the Phyllanthaceae-Epicephala association. *Proceedings of the Royal Society B* 276: 417–426.
- Kuntze O. 1891. *Revisio Generum Plantarum* 2. Klincksieck, Paris, etc.
- Kurz S. 1877. *Forest Flora of British Burma* 2. Office of the Superintendent of Government Printing, Calcutta.
- Lamarck M. 1783. *Encyclopédie Méthodique Botanique* 1, 1. Panckoucke, Paris.
- Li PT. 1987. Notes on the genera *Sauropus* and *Cleistanthus* of Euphorbiaceae in China. *Acta Phytotaxonomica* 25: 132–137.
- Li PT. 1994. Euphorbiaceae-Phyllanthoideae. *Flora Reipublicae Popularis Sinicae* 44, 1. Science Press, Beijing. (In Chinese.)
- Li PT, Chiu H, Ma J, Zhu H, Gilbert MG, et al. 2008. Euphorbiaceae. In: Wu ZY, Raven PH, Hong DY (eds), *Flora of China* 11: 163–314. Science Press, Beijing; Missouri Botanical Garden Press, St. Louis.
- Linnaeus C. 1753. *Species plantarum*. Impensis Laurentii Salvii, Holmiae.
- Linnaeus C. 1767a. *Systema Naturae* ed. 12, 2. Impensis Laurentii Salvii, Holmiae.
- Linnaeus C. 1767b. *Mantissa Plantarum*. Impensis Laurentii Salvii, Holmiae.
- Luo SX, Li YQ, Zhang DX, Renner SS. 2011. Gelechiidae moths are capable of chemically dissolving the pollen of their host plants: first documented spore-pollen breakdown by an animal. *PLoS ONE* 6, 4: e19219. doi: 10.1371/journal.pone.0019219.

- Maddison WP, Maddison DR. 2009. Mesquite: A modular system for evolutionary analysis. Version 2.72. <http://mesquiteproject.org>.
- Manilal KS, Prasannakumar KS, Sivarajan VV. 1985. A new species of *Sauropus* Bl. (Euphorbiaceae) from India. *Journal of the Indian Botanical Society* 64: 294–296.
- McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, et al. (eds). 2012. International code of nomenclature for algae, fungi and plants (Melbourne Code). *Regnum Vegetabile* 154.
- Merrill ED. 1903. *Plantae Ahernianae*. *Bulletin of the Bureau of Forestry, Philippine Islands* 1: 30.
- Merrill ED. 1934. An enumeration of plants collected in Sumatra by W.N. and C.M. Bangham. *Contributions from the Arnold Arboretum of Harvard University* 8: 86.
- Miquel FAW. 1861. *Flora van Nederlandsch Indië. Eerste Bijvoegsel*. Van der Post, Amsterdam, Utrecht.
- Mueller FJH von. 1855. Definitions of rare or hitherto undescribed Australian plants, chiefly collected within the boundaries of the Colony of Victoria. *Transactions of the Philosophical Society of Victoria* 1: 5–24.
- Mueller FJH von. 1859. *Fragmenta Phytographiae Australiae* 1. Joannis Ferris, Melbourne.
- Müller Argoviensis J. 1863. Euphorbiaceae. *Vorläufige Mittheilungen aus dem für DeCandolle's Prodrum bestimmten Manuscript über diese Familie*. *Linnaea* 32: 12–126.
- Müller Argoviensis J. 1866. Euphorbiaceae. In: De Candolle A (ed), *Prodrum Systematis Naturalis Regni Vegetabilis* 15, 2: 189–1260. Masson & Fili, Paris.
- Müller Argoviensis J. 1872. Euphorbiacearum species novae. *Flora* 55: 2–11.
- Pax F, Hoffmann K. 1922. Euphorbiaceae-Phyllanthoideae-Phyllanthaceae. In: Engler A (ed), *Das Pflanzenreich* IV.147.xv: 215–226. Engelmann, Leipzig.
- Pruesapan K, Telford IRH, Bruhl JJ, Draisma SGA, Van Welzen PC. 2008. Delimitation of *Sauropus* (Phyllanthaceae) based on plastid *matK* and nuclear ribosomal ITS DNA sequence data. *Annals of Botany (Oxford)* 102: 1007–1018.
- Pruesapan K, Telford IRH, Bruhl JJ, Van Welzen PC. 2012. Phylogeny and proposed circumscription of *Breynia*, *Sauropus* and *Synostemon* (Phyllanthaceae), based on chloroplast and nuclear DNA sequences. *Australian Systematic Botany* 25: 313–330.
- Radcliffe-Smith A. 1986. Euphorbiaceae. In: Nasir E, Ali SI (eds), *Flora of Pakistan* 172. Pakistan Agricultural Research Council, University of Karachi & Islamabad, Karachi.
- Radcliffe-Smith A. 2001. *Genera Euphorbiacearum*. Royal Botanic Gardens, Kew.
- Rambaut A, Drummond AJ. 2007. *Tracer v1.4* (<http://beast.bio.ed.ac.uk/Tracer> – last checked 20 Nov. 2013).
- Retzius AJ. 1788. *Observationum Botanicarum* 5. Siegfried Lebrecht Crusium, Lipsiae.
- Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed model. *Bioinformatics* 19: 1572–1574.
- Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, et al. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice across a Large Model Space. *Systematic Biology* 61: 1–4.
- Rumphius GE. 1743. *Herbarium Amboinense* 3. Changuion, Catuffe & Uytwerf, Amsterdam, etc.
- Sagun VG, Van der Ham RWJM. 2003. Pollen morphology of the Flueggeinae (Euphorbiaceae, Phyllanthoideae). *Grana* 42: 193–219.
- Samuel R, Kathriarachchi H, Hoffmann P, Barfuss HJ, Wurdack KJ, et al. 2005. Molecular phylogenetics of Phyllanthaceae: evidence from plastid *matK* and nuclear PHYC sequences. *American Journal of Botany* 92: 132–141.
- Sierra SEC, Kulju KKM, Fišer Ž, Aparicio M, Van Welzen PC. 2010. The phylogeny of *Mallotus* s.str. (Euphorbiaceae) inferred from DNA sequence and morphological data. *Taxon* 59: 101–116.
- Sivarajan VV, Balachandran I. 1984. *Sauropus varieri* – A new Euphorbiaceae from India. *Journal of Economic and Taxonomic Botany* 5: 917–919, f. 1–5.
- Smith JJ. 1924. *Plantae novae vel criticae ex Herbario et Horto Bogoriensi* III. *Bulletin du Jardin Botanique de Buitenzorg* ser. 3, 6: 82, 83.
- Sprengel K. 1826. *Systema Vegetabilis* 3. Librariae Dietrichianae, Göttingae.
- Steudel EG. 1841. *Nomenclator Botanicus* ed. 2, 2. Cottae, Stuttgartardiae & Tubingae.
- Thin NN. 1992. Some new species of genera: *Phyllanthus* and *Sauropus* for the Flora of Vietnam. *Journal of Biology (Vietnam)* 14: 16–25.
- Thin NN. 1996. *Euphorbiaceae of Vietnam*. Publishing House, Hanoi.
- Thin NN. 2007. *Taxonomy of Euphorbiaceae in Vietnam*. Vietnam National University Publisher, Hanoi.
- Thwaites GHK. 1861. *Enumeratio Plantarum Zeylaniae* 4. Dulau & Co., London.
- Thwaites GHK. 1864. *Enumeratio Plantarum Zeylaniae* 5. Dulau & Co., London.
- Van Welzen PC. 2001. Two new species of *Sauropus* (Euphorbiaceae) from Thailand, and a new combination. *Blumea* 46: 499–504.
- Van Welzen PC. 2003. Revision of the Malesian and Thai species of *Sauropus* (Euphorbiaceae: Phyllanthoideae). *Blumea* 48: 319–391.
- Van Welzen PC, Chayamarit K. 2001. Two new *Mallotus* and two new *Sauropus* species (Euphorbiaceae) endemic to Thailand. *Kew Bulletin* 56: 649–656.
- Van Welzen PC, Esser H-J. 2005. *Breynia*. In: Chayamarit K, Van Welzen PC (eds), *Flora of Thailand* 8, 1: Euphorbiaceae (genera A–F): 132–141. The Forest Herbarium, Bangkok.
- Van Welzen PC, Haegens RMAP, Slik JWF, Bollendorff SM, Dressler S, Esser H-J. 2000. Checklist of the genera of Thai Euphorbiaceae – I. *Thai Forest Bulletin (Botany)* 28: 59–111.
- Van Welzen PC, Pruesapan K. 2010. Four new species of *Breynia* (Phyllanthaceae/Euphorbiaceae sensu lato) and one new combination from Thailand and Malaysia. *Thai Forest Bulletin (Botany)* 38: 111–119.
- Vorontsova MS, Hoffmann P. 2008. A phylogenetic classification of tribe Poranthereae (Phyllanthaceae, Euphorbiaceae sensu lato). *Kew Bulletin* 63: 41–59.
- Wagner WL, Lorence DH. 2011. A nomenclator of Pacific oceanic island *Phyllanthus* (Phyllanthaceae), including *Glochidion*. *PhytoKeys* 4: 67–94.
- Webster GL. 1960. The status of *Agyneia* and *Glochidion* (Euphorbiaceae). *Taxon* 9: 25, 26.
- Webster GL. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Annals of the Missouri Botanical Garden* 81: 33–144.
- Webster GL, Carpenter KJ. 2008. Pollen morphology and systematics of palaotropical *Phyllanthus* and related genera of subtribe Phyllanthinae (Euphorbiaceae). *Botanical Journal of the Linnean Society* 157: 591–608.
- Wheeler LC. 1975. Euphorbiaceae genera lectotyped. *Taxon* 24: 534–538.
- Wiens JJ. 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology* 53: 653–661.
- Wight R. 1852. *Icones Plantarum Indiae Orientalis* 5. Franck & Co., Madras.
- Wight R. 1853. *Icones Plantarum Indiae Orientalis* 6. Franck & Co., Madras.
- Willdenow CL. 1805. *Species Plantarum* 4. Nauk, Berolini.