Disentangling a complex genus: systematics, biogeography and bioactivity of the genus Phyllanthus L. and related genera of tribe Phyllantheae (Phyllanthaceae)

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Citation

Bouman, R. W. (2022, December 6). *Disentangling a complex genus: systematics, biogeography and bioactivity of the genus Phyllanthus L. and related genera of tribe Phyllantheae (Phyllanthaceae)*. Retrieved from https://hdl.handle.net/1887/3492676

CHAPTER 7

Molecular phylogenetics of *Phyllanthus* sensu lato (Phyllanthaceae): towards coherent monophyletic taxa

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Published in Taxon 70 (1): 72-98. 2021

https://doi.org/10.1002/tax.12424

Chapter 7

Molecular phylogenetics of *Phyllanthus* sensu lato (Phyllanthaceae): towards coherent monophyletic taxa

Short title: Phylogenetics of the genus *Phyllanthus*

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Abstract

The genus *Phyllanthus* is paraphyletic as currently circumscribed, with the genera *Breynia*, *Glochidion* and *Synostemon* nested within it. A phylogeny based on nuclear (ITS, *PHYC*) and chloroplast (*matK*, *accD-psaI*, *trnS-trnG*) markers is presented, including 18/18 subgenera and 53/70 sections. Differences in habit, branching type, floral and fruit characters are discussed, and we find indications for shifts in pollination and dispersal strategies possibly underlying the convergent evolution of these characters in multiple clades. Several taxonomic issues were found in the subgeneric classification of Phyllanthus that will require new transfers and rank changes. *Phyllanthus* subg. *Anesonemoides*, subg. *Conami*, subg. *Emblica*, subg. *Gomphidium*, subg. *Kirganelia* and subg. *Phyllanthus* are polyphyletic, and several sections appear to be paraphyletic (e.g., *P.* sect. *Anisonema*, sect. *Emblicastrum*, sect. *Pseudoactephila*, sect. Swartziani, and sect. *Xylophylla*); *P.* subg. *Phyllanthodendron* is furthermore paraphyletic with the genus *Glochidion* nested within. To create a classification of tribe Phyllantheae that comprises exclusively monophyletic taxa, it is necessary to treat several clades at the same taxonomic rank as the genera *Breynia*, *Glochidion* and *Synostemon*. Since combining all genera would lead to one giant heterogeneous genus that is difficult to define, we recommend dividing *Phyllanthus* into several monophyletic genera, which have previously

been recognized and often possess diagnostic (combinations of) morphological characters. This new classification is forthcoming.

Keywords: molecular phylogenetics; paraphyly; Phyllanthaceae; *Phyllanthus*; sections; subgenera; systematics

Introduction

The pantropical family Phyllanthaceae is the second-most species-rich segregate fromEuphorbiaceae sensu lato, to be recognized since the publication of APG II (2003). It currently consists of about 2000 species, with more than 1200 placed in the largest tribe Phyllantheae Dumort (Govaerts *et al.* 2000; Hoffmann *et al.* 2006). Phyllantheae have been the focus of extensive discussion concerning the relationships and circumscriptions of genera (e.g., Hoffmann *et al.* 2006; Pruesapan *et al.* 2012; Van Welzen *et al.* 2014a).

Previous phylogenetic studies that focused specifically on the Phyllanthaceae sought to elucidate the structure of the various tribes (mostly of subfamily Phyllanthoideae) (e.g., Kathriarachchi *et al.* 2005, 2006; Samuel *et al.* 2005; Vorontsova *et al.* 2007), leading to revised classifications of the tribes Phyllantheae (Hoffmann 2008; Ralimanana & Hoffmann 2011, 2014; Ralimanana *et al.* 2013; Van Welzen *et al.* 2014a), Poranthereae (Vorontsova & Hoffmann 2008, 2009) and Wielandieae (Hoffmann & McPherson 2007). However, tribe Phyllantheae remains problematic, mainly because the largest genus, *Phyllanthus* L., is paraphyletic (Kathriarachchi *et al.* 2006).

Phyllanthus contains more than 800 species and has a complex taxonomic history (Govaerts *et al.* 2000; Bouman *et al.* 2018a). The main characters used to distinguish *Phyllanthus* from other genera are the absence of corolla, pistillodes and staminodes; the presence of a disc or disc glands in the flowers and a specialized branching system called phyllanthoid branching (Webster 1956) that is present in the majority of species. Species with phyllanthoid branching have deciduous floriferous branchlets subtended by reduced scale-like leaves (cataphylls) (Fig. 7-1F) and lack laminate leaves on the main stem (Webster 1956). The genus is morphologically very diverse and shows a large range in habit, flower, seed and pollen morphology (Webster, 1956; Punt, 1967, 1972, 1980, 1986, 1987; Meeuwis & Punt, 1983; Lobreau-Callen *et al.* 1988; Stuppy, 1996; Webster & Carpenter, 2002, 2008; Kathriarachchi *et al.* 2006). Several morphological characters seem to have evolved or were lost more than once (Kathriarachchi *et al.* 2006; Falcón *et al.* 2020), however, rendering the taxonomy complex and identifications difficult. Phyllanthus was shown to be paraphyletic in recent studies, with the genera *Synostemon* F.Muell., *Breynia* J.R.Forst.&G.Forst. (including *Sauropus* Blume) and *Glochidion* J.R.Forst. & G.Forst. nested within it. First indications of paraphyly were found by Wurdack *et al.* (2004) and Samuel *et al.* (2005), but the sample sizes were inadequate for effecting taxonomic changes at the generic level (Kathriarachchi *et al.* 2006).

During subsequent studies of tribe Phyllantheae with increased sampling, including the majority of subgenera and sections of Phyllanthus, it was confirmed that the genus was indeed paraphyletic (Kathriarachchi *et al.* 2006; Falcón *et al.* 2020).

Several solutions have been proposed by various authors for handling paraphyletic taxa. Some vouch for the acceptance of paraphyletic taxa (e.g., Brummitt 2002, 2003; Hörandl 2007), while most taxonomists favour recognizing exclusively monophyletic taxa, either by subsuming (e.g., Larridon *et al.* 2011; Khanum *et al.* 2016; Bruyns *et al.* 2017) or dividing (e.g., Ehrendorfer & Barfuss, 2014; Manning *et al.* 2014) previously established classifications. The first solution was proposed by Kathriarachchi *et al.* (2006), resulting in *Breynia*, *Glochidion* and *Synostemon* being subsumed into *Phyllanthus* to create a single giant genus of more than 1200 species (Hoffmann *et al.* 2006). New names for local floras were published by several authors who followed their decision (e.g., Chakrabarty & Balakrishnan 2009b; Wagner & Lorence 2011; Kurosawa 2016; Govaerts 2018). However, others feel that this would only push the problems to the subgeneric level (Pruesapan *et al.* 2008; Van Welzen *et al.* 2014a). They suggested that a more representative phylogeny would be needed to explore the option of creating new monophyletic and morphologically recognizable genera (e.g., Pruesapan *et al.* 2008). An analysis with increased sampling of the genera nested within Phyllanthus showed that *Glochidion* was monophyletic, but that Breynia should be combined with Sauropus and that the Australian genus *Synostemon* should be resurrected (Pruesapan *et al.* 2008, 2012; changes implemented in Chakrabarty & Balakrishnan 2012, 2015; Van Welzen *et al.* 2014a). As a consequence, the genus *Phyllanthus* remains paraphyletic, but with many morphologically defined subgenera and sections that are potential candidates for new or reinstated genera. Despite the body of work leading up to and including Van Welzen *et al.* (2014a), there has been some reluctance to follow the revised classification of Synostemon and Breynia due to the issue of the non-monophyly of *Phyllanthus* (Kato & Kawakita 2017; Govaerts 2018).

Due to its diversity in habit, flower, pollen and seed morphology (Fig. 7-1), the genus *Phyllanthus* is currently divided into 18 subgenera with 70 sections and 14 subsections (Bouman *et al.* 2018a). The first species within the genus were described by Linnaeus (1753), from Neotropical and Indian material. Soon after, many new genera were defined based on differences in flower morphology, specifically the number and fusion of the stamens in staminate flowers (e.g., Jussieu 1824; Baillon 1858). A major change was undertaken by Müller (1863, 1865, 1866), who combined over 10 genera into *Phyllanthus* s.l. with more than 40 sections. The genus *Glochidion* was considered to be closer to *Phyllanthus* than *Breynia* or *Sauropus* and was therefore combined with *Phyllanthus* (Müller 1866), but was segregated again by Hooker (1887). Müller's (1866) classification was further modified by Webster (1979), who reinstated the genus *Margaritaria* L.f. in his revision of *Phyllanthus* from the West Indies. Webster (1956, 1957, 1958) utilized previously established sections and subgenera (Kurz 1873; Croizat & Metcalf 1942) to create a provisional hierarchical classification of subgenera and sections to show the relations between groups. This classification scheme was subsequently expanded by Webster himself (Webster 1967b, 1970, 1978, 1986, 1995, 2001a, 2001b, 2002a, 2002b, 2003, 2004) and various authors in the treatment of *Phyllanthus* for other areas such as Africa (Brunel & Roux 1977, 1985; Brunel 1987), Malesia (Airy Shaw 1971, 1975, 1980) and New Caledonia (Schmid 1991). The main characters for this classification were differences in flower, fruit and pollen morphology, and the presence or absence of phyllanthoid branching (Webster 1956). The congruence of this morphology-based classification with molecular phylogenies was evaluated by Kathriarachchi *et al.* (2006) and Falcón *et al.* (2020). Several subgenera were found to be polyphyletic, although most of these issues were addressed in subsequent revisions (Webster 2007; Ralimanana & Hoffmann 2011, 2014; Ralimanana *et al.* 2013).

Previous classifications and results from phylogenetic studies and subsequent revisions were summarized by Bouman *et al.* (2018a) (and only a minority of species could not yet be classified due to incomplete data). Previous samplings in phylogenetic studies by Kathriarachchi *et al.* (2006) and Falcón *et al.* (2020) have only covered about 10% of the genus. To settle the debate as to whether it is possible to render the undiagnosable *Phyllanthus* into morphologically diagnosable, monophyletic taxa, a thoroughly sampled phylogenetic analysis of the genus is needed. Such a phylogeny should provide a sound examination of the classification presented by Bouman *et al.* (2018a). In the present study, we include a much higher sampling, with 220 of the 881 species, with a complete sampling at the subgeneric level (18/18) and with 53 of the currently 70 recognized sections. The subgeneric classification of the species of Phyllanthus included here follows Bouman *et al.* (2018a).

Materials and methods

Taxon sampling

Increased sampling efforts were undertaken to include *Phyllanthus* species from the entire distribution range and the majority of taxonomically defined subgroups. Additional sequences used in other studies were obtained from GenBank (Appendix 7-1). Most of the previously unsampled groups listed by Kathriarachchi *et al.* (2006: Table 7-1) were included. Recently collected silica-gel dried leaf samples were obtained from various contributors from botanical gardens in Europe, Africa and Asia (see Acknowledgments); other DNA samples were obtained from herbarium material. A full list of all samples is given in Appendix 7-1. Ingroup sampling included 32 species of Breynia (43 samples), 7 species of *Synostemon* (10 samples), 12 species of *Glochidion* (15 samples) and 221 species of *Phyllanthus* (312 samples). Several species of *Antidesma* L., *Bridelia* Willd., *Flueggea* Willd., *Heterosavia* (Urb.) Petra Hoffm., *Margaritaria*, *Notoleptopus* Voronts. & Petra Hoffm. and *Plagiocladus* Jean F.Brunel were used as outgroups (selection based on previous phylogenies: Wurdack *et al.* 2004; Pruesapan *et al.* 2008).

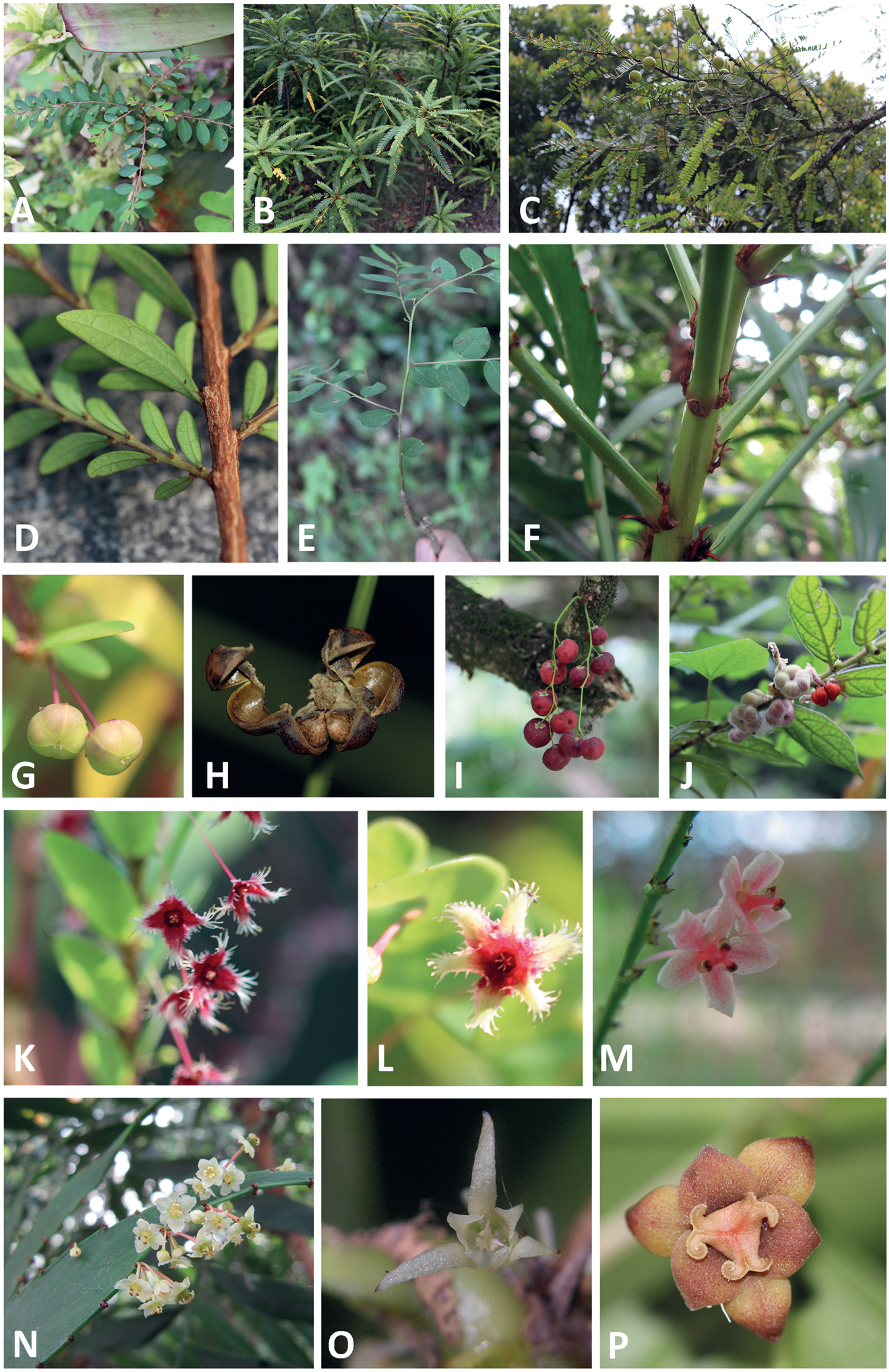
A
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Figure 7-1. Major characters of *Phyllanthus* and related genera *Breynia* and *Glochidion*. A. habit of the herbaceous *P. tenellus* (subgenus *Tenellanthus*); B. habit of *P. watsonii* (subgenus *Eriococcus*); C. habit and fruits of *P. emblica* (subgenus *Emblica*); D. non-phyllanthoid branching in *P. myrtellus*, note the leaves subtending lateral branches (subgenus *Macraea*); E. sub-phyllanthoid branching in a young plant of *P. glaucus*, lateral branches are deciduous (subgenus *Kirganelia*); F. phyllanthoid branching and phylloclades in *P. arbucula* (subgenus *Xylophylla*); G. young capsules of *P. myrtellus* (subgenus *Macraea*); H. dehisced capsule of *P. juglandifolius* (subgenus *Xylophylla*); I. berries on a specialized leafless branchlet of *P. microcarpus* (subgenus *Kirganelia*); J. capsules of *G. eriocarpum* with orange arillate seeds exposed in some (*Glochidion*); K. staminate flowers of *P. pulcher* (subgenus *Eriococcus*); L. pistillate flowers of *P. pulcher* (subgenus *Eriococcus*); M. flowers of *P. mimosoides* (subgenus *Xylophylla*); N. flowers of *P. arbuscula* (subgenus *Xylophylla*); O. staminate flower of *P.* cf. *poilanei* (subgenus *Phyllanthodendron*); P. pistillate flower of *B. androgyna* (*Breynia*). Photos A, C–G, I–M,N & P by R.W.Bouman; photo B © R.-Y. Yu; photo H by J.S. Strijk; photo O ©M.S. Nuraliev .

DNA extraction, amplification and sequencing

DNA was extracted from fresh material using the DNeasy Plant Mini kit (Qiagen, Hilden, Germany) following the manufacturer's protocol, with a modified protocol (Wurdack *et al.* 2004) adopted for herbarium material. Modifications consisted of an extended lysis step from 10 min to 12–24 h with the addition of 20 mg/ml proteinase K and 6.5% β-mercaptoethanol. The final elution was extended to 2 × 30 min with each elution step undertaken with only 40 µl AE buffer. Collection and voucher data are presented in Appendix 7-1. Other samples were extracted with the NucleoMag 96 Tissue kit (Macherey- Nagel, Düren, Germany) following the manufacturer's protocol using a KingFisher Flex magnetic particle processor (Thermo Scientific, Waltham, Massachusetts, U.S.A.), but with an extended lysis step of 12–24 h.

Two nuclear (high-copy spacer ITS, low-copy *PHYC*) and three chloroplast (*accD-psaI*, *trnS-trnG* intergenic spacers, *matK* with the *trnK* intron) DNA markers were selected for use in this study based on variability and to complement previously generated data (e.g., Kathriarachchi *et al.* 2006; Kawakita & Kato 2009; Pruesapan *et al.* 2008, 2012). Primers are shown in Table 7-1. Polymerase chain reactions (PCR) were performed in volumes of 25 µl consisting of: 15.25 µl Milli-Q H_2O, 2.5 µl 50× PCR Buffer, 1 µl 50 mM of $MgCl_2$, 1 µl each of forward and reverse primers (10 mM), 2 µl 2.5 mMdNTP, 1 µl 10 µg/µl bovine serum album (BSA), 0.25 µl KlearTaq and 1–2 µl of DNA. A standard PCR program was used for amplification, with an initial denaturation for 2 min at 94°C; 40 cycles of 1 min

Table 7-1. Primer sequences for the amplification of the various markers with annealing temperatures and references. Primers designed during this study are designated with DH (designed here).

Primer	Forward or reverse primer	Sequence (5' - 3')	Annealing temperature (°C)	Source article
PHYC-F	Forward	CCAGCTACTGATATACCTCAAGCTTC	48	Samuel *et al.* 2005
PHYC-R	Reverse	CCAGCTTCCATAAGGCTATCAGTACT	48	Samuel *et al.* 2005
PHYC-178F	Forward	TGGGTAC(AGT)AT (GT)GCATCTCTTG	55	DH
PHYC-260F	Forward	AAAATTGTGGGGCTTGGTGG	55	DH
PHYC-439F	Forward	TGCT(CT)CT(CT)AGAGATGCACCT	55	DH
PHYC-260Rev	Reverse	CCACCAAGCCCCACAATTTT	55	DH
PHYC-344Rev	Reverse	CCTGAAC(AC)CCAAACACTTGC	55	DH
PHYC-490Rev	Reverse	CTCCRTCACACTTAACTA(AG)(AG)TCCA	55	DH
ITS5	Forward	GGAAGTAAAAGTCGTAACAAGG	52,5	White *et al.* 1990
ITS4	Reverse	TCCTCCGCTTATTGATATGC	52,5	White *et al.* 1990
ITS2	Reverse	GCTGCGTTCTTCATCGATGC	52,5	White *et al.* 1990
ITS3	Forward	GCATCGATGAAGAACGCAGC	52,5	White *et al.* 1990
accD	Forward	AAT(CT)GTACCACGTAATC(CT)TTTAAA	49	Shaw *et al.* 2007
psaI-75R	Reverse	AGAAGCCATTGCAATTGCCGGAAA	49	Small *et al.* 1998
accd-121F	Forward	AGCAAAATAAAAT(AG)CGAAGAGTG	55	DH
accd-151F	Forward	ACGAAAGCCCTATCAACAAGAGA	50	DH

accd-226R	Reverse	CTCTTGTTGATAGGGCTTTCGT	50-55	DH
accd-462Rev	Reverse	TCTGCTCCCGAGAAATTCGT	48	DH
accd-595Rev	Reverse	GGAGTGTAGAACTAAGTAAATGGACT	50-55	DH
trnS-F	Forward	GCCGCTTTAGTCCACTCAGC	55	Hamilton 1999
trnG-R	Reverse	GAACGAATCACACTTTTACCAC	55	Hamilton 1999
trnSG-448F	Forward	CCATTTCCATGACCTAGCCCAA	55	DH
trnSG-535R	Reverse	TTCGAATCGAAGAAATCCTTTTATCT	55	DH
trnK-570F	Forward	TCCAAAATCAAAAGAGCGATTGG	55	Samuel *et al.* 2005
matK80F	Forward	CTATACCCACTTATCTTTCGGGAGT	55	Samuel *et al.* 2005
matK390F	Forward	CGATCTATTCATTCAATATTTC	55	Samuel *et al.* 2005
matK800F	Forward	CATGCATTATGTTAGATATCAAGG	55	Samuel *et al.* 2005
matK1200F	Forward	GA(CT)TCTGATATTATCAACCGATTTG	55	Samuel *et al.* 2005
matK190R	Reverse	ATTCGAGTAATTAAACGTTTTACAA	55	Samuel *et al.* 2005
matK530R	Reverse	GTTCCAATTCCAATACTCGTGAAG	55	Samuel *et al.* 2005
matK950R	Reverse	AAAAT(AG)ACATTGACATAAATTGACAA(AG)G	55	Samuel *et al.* 2005
matK1300R	Reverse	CGAAGTATATA(CT)TT(CT)ATTCGATACA	55	Samuel *et al.* 2005
matK1710R	Reverse	GCTTGCATTTTTCATTGCACACG	55	Samuel *et al.* 2005

denaturation at 94°C, annealing for 30 s with the annealing temperature specific for each primer (see Table 7-1) and elongation for 1 min at 72°C; and a final elongation step of 10 min at 72°C. New internal primerswere designed for the *PHYC*, *accD-psaI* and *trnS-trnG* markers in order to amplify the marker in smaller segments, which proved to be more effective when working with herbarium material. Primers were designed using sequences from several *Breynia*, *Glochidion*, *Phyllanthus*, and *Synostemon* species with the online application Primer3Plus (bioinformatics.nl/cgi-bin/primer3plus/ primer3plus.cgi) with default settings (Fig. 7-2).

The length of PCR fragments was verified on a 1%agarose gel with electrophoresis. Successful PCR samples were subsequently analyzed on either an ABI3730xl automated sequencer (Applied Biosystems, Forster City, California, U.S.A.) by using ABI BigDye terminator chemistry, or aMegaBACE 1000 automated sequencer (Amersham Bioscience, now GE Healthcare Europe, Diegem, Belgium) using DYEnamic ETDye Terminators chemistry following the manufacturers' protocols by another company (BaseClear, Leiden, the Netherlands). Primer combinations used during sequencing were dependent on DNA quality, and markers of herbarium specimens were often amplified in segments of 200–300 nucleotides.

Sequence cleaning, alignment and resulting datasets

Forward and reverse sequences were combined, primers trimmed and cleaned of reading errors using the program Sequencher v.4.14 (GeneCodes Corp., http://www.genecodes.com/) and aligned using the program ClustalW v.2.1. (Larkin *et al.* 2007) on the CIPRES (Cyber Infrastructure for Phylogenetic RESearch) gateway (https://phylo.org/) using default settings. The subsequent alignment file was checked and manually corrected using a similarity criterion for obvious alignment errors in PAUP v.4.0a (Swofford, 2002). Some ambiguous alignment positions were encountered in the *trnS-trnG* spacer, which varied greatly in sequence length from positions 259 to 413 in the alignment, and these were excluded before analysis.

For analysis, ends of the data matrices (suppl. Appendices S1–S5) were truncated to match sequences generated here and those retrieved from GenBank. The individual marker trees (suppl. Figs. 7-S1 – 7-S7) were visually inspected for incongruence before combining the datasets. Several species were included from GenBank or with only partial sequences obtained from herbarium species; this resulted in some missing data for a number of taxa (see Appendix 7-1). To check for the effect of missing data on the relationships between major groups, two separate datasets were prepared. A full dataset, which contained all specimens from the individual marker analyses and a trimmed dataset that only included samples of which at minimum four of the five markers were sequenced. The full dataset contained 396 terminals, while the trimmed dataset contained 290 terminals.

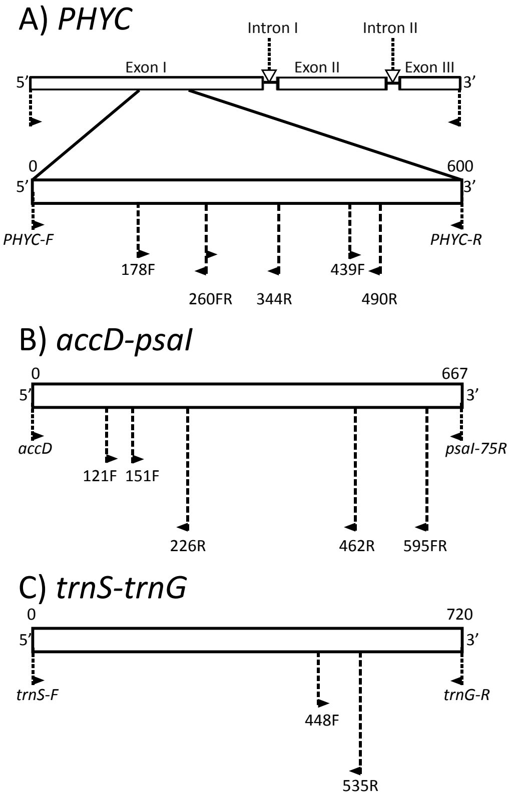


Figure 7-2. Schematic design for the spacer *PHYC* (A), *accD–psaI* (B) and *trnS–trnG* (C) spacer with newly designed primers indicated by arrowheads. Number behind primer names indicates approximate nucleotide position within the marker including insertions in the matrix. *PHYC* figure adapted from Samuel *et al.* (2005).

Phylogenetic analyses

Analyses of the individual markers, the combined and combined reduced datasets were run under Bayesian inference using MrBayes v.3.2.7 (Ronquist *et al.* 2012) and maximum likelihood using RAxML v.8.2.12 (Stamatakis, 2014) via the CIPRES gateway.Missing sequences due to amplification problems or those that could not be obtained from GenBank, were recorded as missing data following Wiens (2003). MrModeltest v.2 (Nylander 2004) was used on the dataset for each marker set to obtain the best-fitting model for Bayesian inference. All best models were the mostparameterized models, which include a Gamma distribution (Γ) (coded as: nst = 6, rates = gamma for ITS, *accD-psaI* and *trnS-trnG*, rates = equal for *PHYC* and *matK*), and all individual analyseswere run for 10 million generations on two parallel runs of four Markov chains (CIPRES default). An initial burnin of 25% was used. Each marker was run as a separate partition in the concatenated

Table 7-2. Summary of individual marker datasets used in the analyses. Number of generated sequences shows between brackets the number of missing nucleotide sequences.

Marker	Nr. of sequences in dataset (Missing)	Max. sequence length (bp)	Alignment length (bp)	Nr of informative sites
ITS	352 (42)	304-650	732	451
PHYC	335 (49)	134-581	589	329
matK	369 (35)	732-1791	2170	1179
accD-psaI	321 (73)	197-546	1036	552
trnS-trnG	272 (122)	209-635	1233 (1078)	732

matrix following previously determined rates. Effective sampling sizes (ESS) and convergence of the two runs were checked via the resulting ".p" files using Tracer v.1.7.1 (Rambaut & Drummond, 2018). The maximum likelihood tree was reconstructed under the GTRCAT model and CIPRES default settings to accelerate computation of our dataset. The analysis was run with a concatenated dataset partitioned by marker with 1000 bootstrap iterations.

Results

Analysis of the individual and combined nuclear/combined chloroplast markers

Due to the use of herbarium material and data available from GenBank, the majority of taxa lacked comprehensive data for all markers. Table 7-2 shows the number of contigs for each marker and the number of informative sites. We generated 1349 new sequences during this study and included 300 sequences from GenBank. Non-coding regions such as the *accD-psaI* spacer had many more gaps than the coding region of *PHYC*. Results for individual markers recovered similar clades, but lacked adequate support to provide reliable and stable relationships between clades. Clade A (Figs. 7-3, 7-4; suppl. Figs. S1–S7) was recovered as sister to the remainder of the genus *Phyllanthus* with maximum support (suppl. Fig. 7-S7-7-S3; PP 1.0) in the ITS topology, but with lower support in the other markers. There is consistently high support for clade B (PP > 0.99), but resolution within the clade differs between markers. *Phyllanthus* subg. *Kirganelia* (A.Juss.) Kurz (clade C1 in Fig. 7-4; PP 1.0) was consistently retrieved as sister to a clade comprising subg. *Eriococcus* (Hassk.) Croizat & Metcalf (clade C3) and sect. *Lysiandra* (F.Muell.) G.L.Webster + sect. *Antipodanthus* G.L.Webster (C2; discussed below) (PP > 0.66) (suppl. Figs. 7-S3–7-S7, except in suppl. Fig. 7-S4). The relationships between clades D, E and F (Fig. 7-4) were generally poorly supported, although clade D was confirmed as monophyletic in most datasets (PP > 0.89) except for the nuclear, ITS, *PHYC* and *accD-psaI* topologies. Support for the relationship between *P.* subg. *Phyllanthodendron* and *Glochidion* was obtained from all markers (clade H; PP 1.0). Similarly, the relationship between the genera *Breynia* and *Synostemon* was also recovered in all markers (clade I; PP > 0.97), except for trnS-trnG, where it was part of a larger polytomy with the genus *Glochidion*.

Incongruence

During the Bayesian analyses of the individual markers, some incongruence was found, but mostly between chloroplast and nuclear markers. The most significant incongruence found was between the ITS dataset (suppl. Fig. 7-S3) and the other four markers (suppl. Figs. 7-S4–7-S7) and affected mainly *Phyllanthus* subg. *Gomphidium* (Baill.) G.L. Webster and subg. *Betsileani* (Jean F.Brunel) Ralim. & Petra Hoffm. *Phyllanthus* subg. *Betsileani* was recovered as sister to subg. *Gomphidium* sect. *Gomphidium* and sect. *Nymania* (suppl. Fig. 7-S3; PP 1.0), while in the concatenated dataset, these taxa were in the neighbouring clades F2 and F1, respectively (Fig. 4). In the analysis of *PHYC*, *accD-psaI*, *matK* and our concatenated datasets (except concatenated nuclear dataset), *P.* subg. *Betsileani* was always recovered as sister to other species of Madagascar from subg. *Menarda* and part of subg. *Anesonemoides* and subg. *Gomphidium*. Kathriarachchi *et al.* (2006) opted to exclude ITS sequences of *P.* subg. *Betsileani* in their concatenated analysis. Branch lengths were here observed to be quite short, indicative of a more recent split, with the ITS marker lacking accumulated additional mutations. We, therefore, decided to combine the datasets without excluding specific markers for certain species, resulting in a consensus tree of all markers that showed a similar relationship between *P.* subg. *Gomphidium*, subg. *Anesonemoides*, subg. *Betsileani* and subg. *Menarda* (Comm. ex A.Juss.) Ralim. & Petra Hoffm. (Clade F) to that found in the *PHYC* and chloroplast marker sets. The nuclear (suppl. Fig. 7-S1) and chloroplast (suppl. Fig. 7-S2) datasets differed in the relationship between clades D–F. In the nuclear phylogeny, clade F is sister to clades D, E & G–I (suppl. Fig. 7-S1; PP 0.99), while the chloroplast phylogeny is similar to the concatenated dataset with clade D sister to clades E–I (suppl. Fig. 7-S2; Fig. 4). Additional incongruence was found in the relationships between P. subg. *Tenellanthus*, subg. *Swartziani* and subg. *Afroswartziani* (Fig. 7-4, clade D; but see suppl. Figs. 7-S1 & 7-S2). In the chloroplast dataset, *P.* subg. *Swartziani* is recovered as sister to a clade comprising subg. *Tenellanthus* and subg. *Afroswartziani*. This is in contrast with the combined dataset (Fig. 4), in which *P.* subg. *Tenellanthus* is recovered as sister to the other subgenera.

Concatenated datasets

Our total dataset of all markers combined resolved *Phyllanthus* in eight major clades (Figs. 7-3, 7-4; suppl. Fig. 7-S8), but the genus, like in all former analyses, was found

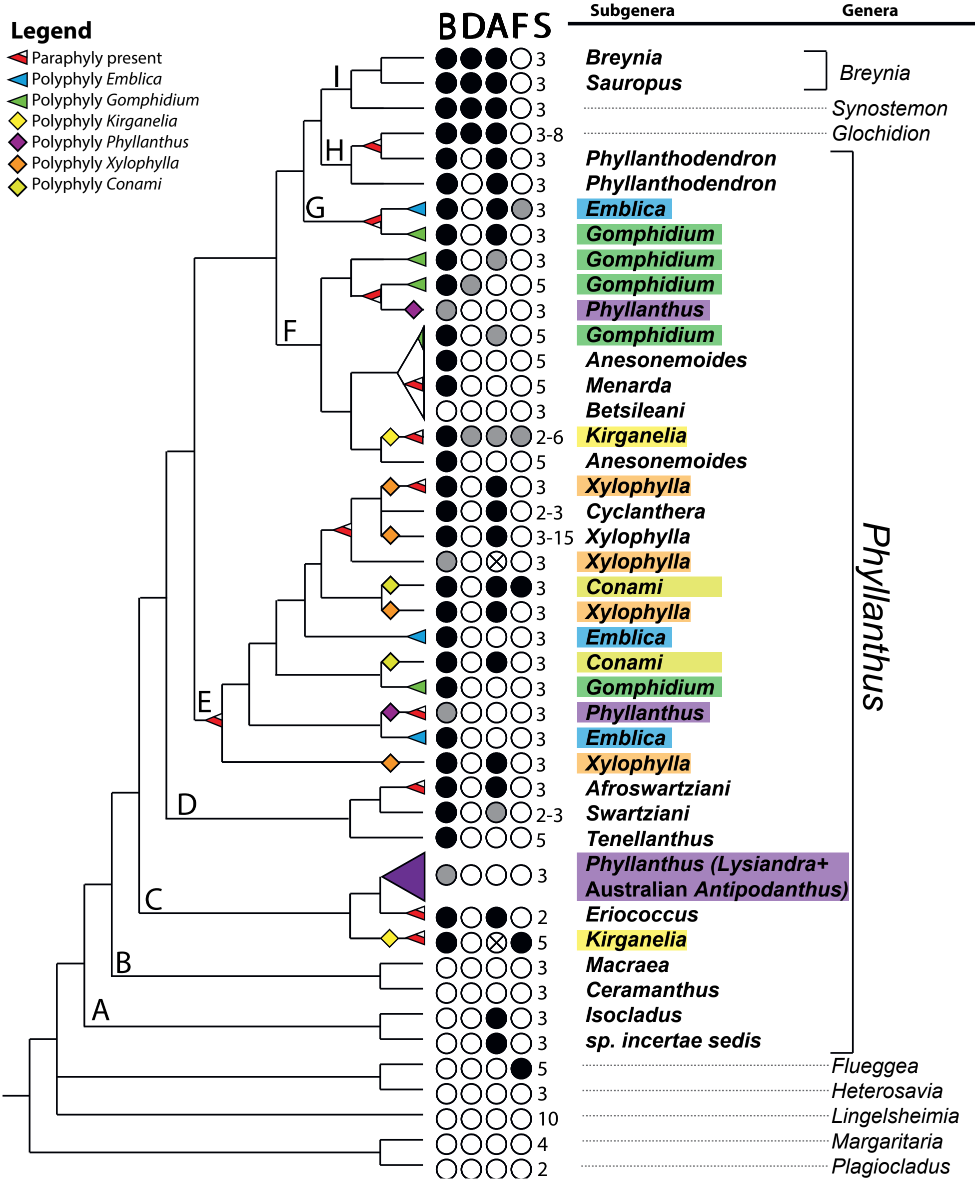


Figure 7-3. Molecular phylogenetic relationships of tribe Phyllantheae, simplified from Fig. 7-4 showing genera and subgenera. Colouring of clades follow Fig. 7-4 and paraphyly is highlighted with a red triangle (◀). Several morphological characters and character states are shown: (B) branching non-phyllanthoid (○), sub-phyllanthoid (●) or phyllanthoid (●); (D) disc present (○), absent (●) or when both variations occur in the clade (●); (A) androphore filaments free (○), fused (●) or when both are present (●),whorled stamens (⊗); (F) fruit capsules (○), or berries (●); (S) average stamens number.

to be paraphyletic. While the majority of relationships between groups remained largely unchanged (Figs. 7-3, 7-4), internal support of species relations within major groups differed between the analyses of the total and reduced datasets. Posterior probabilities of major nodes differed, and clade E was more resolved in the analysis of the reduced dataset (suppl. Fig. 7-S8). The relationship between clades A–I did not differ when comparing the reduced dataset with the total dataset. In Fig. 7-4, the relationship between clades E1, E2 and E3 was not resolved. In the reduced dataset (suppl. Fig. 7-S8), clade E2, including *P.* subg. *Conami* sect. *Nothoclema* G.L. Webster and subg. *Emblica* sect. *Microglochidion* (Müll. Arg.) Müll.Arg., was resolved as sister to clade E3 (PP 0.89). This might be an artifact of the number of markers available for taxa in clade E in the total dataset. The reduced dataset also achieves greater resolution of clade F, particularly in *P.* subg. *Gomphidium* and the relationship between its sections *Gomphidium* and *Nymania*. *Phyllanthus* sect. *Nymania* is found to be paraphyletic (see suppl. Fig. 7-S8) with sect. *Gomphidium* nested within (PP 1.0). Other clades did not show changes in the relationships between major groups in the reduced dataset, with only support levels differing between matrices.

Comparing Bayesian inference (Fig. 7-4) with maximum likelihood (suppl. Fig. 7-S9) of our total dataset did not result in significant differences. The same larger clades A–I were retrieved (though weakly supported for the relationship between clades D–G). Internal relationships between species differed slightly, often not significantly (BP < 50). Aside from differences in node support, clades A–D, did not differ between Bayesian inference and maximum likelihood. Clade E was similarly resolved between the two analysis methods, but was more weakly supported in the ML analysis. The support for the relationship between clades E1–E3 was too low to be informative. Similar to the analysis of our reduced dataset (suppl. Fig. 7-S8), part of *P.* subg. *Gomphidium* sect. *Nymania* was found to be sister to all other species of sect. *Gomphidium*, but other relationships within this part of clade F2 were only resolved with low support. Aside from internal relationships between species (with weak support, BP < 50), clade G–I did not differ between Bayesian inference and maximum likelihood.

Discussion

Phyllanthus is a paraphyletic conglomerate of multiple subgenera and (sub) sections, which together are presently classified as one genus. *Glochidion* and *Breynia* (including *Sauropus* and previously *Synostemon*) were treated separately on the basis of a loss of the nectar disc (*Glochidion*, part of *Synostemon*) or due to a functional change, with disc glands becoming scales that close the staminate flowers until the pollen is mature (part of *Breynia*, part of *Synostemon*) (Radcliffe- Smith, 2001; Van Welzen *et al.* 2014a). For a sound discussion on any possible combination or separation, the flaws of the current system need to be discussed, as well as the morphological distinctness of the various groups and clades. Floral convergence or

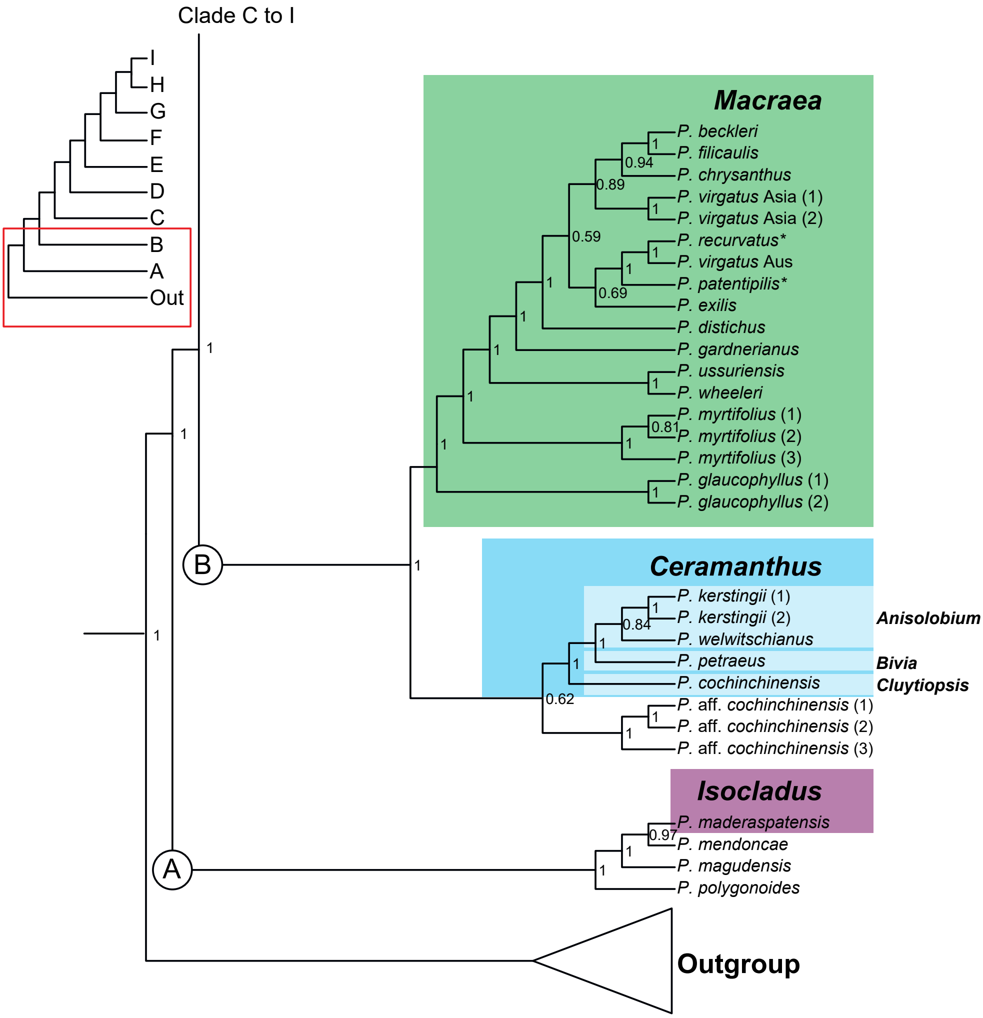
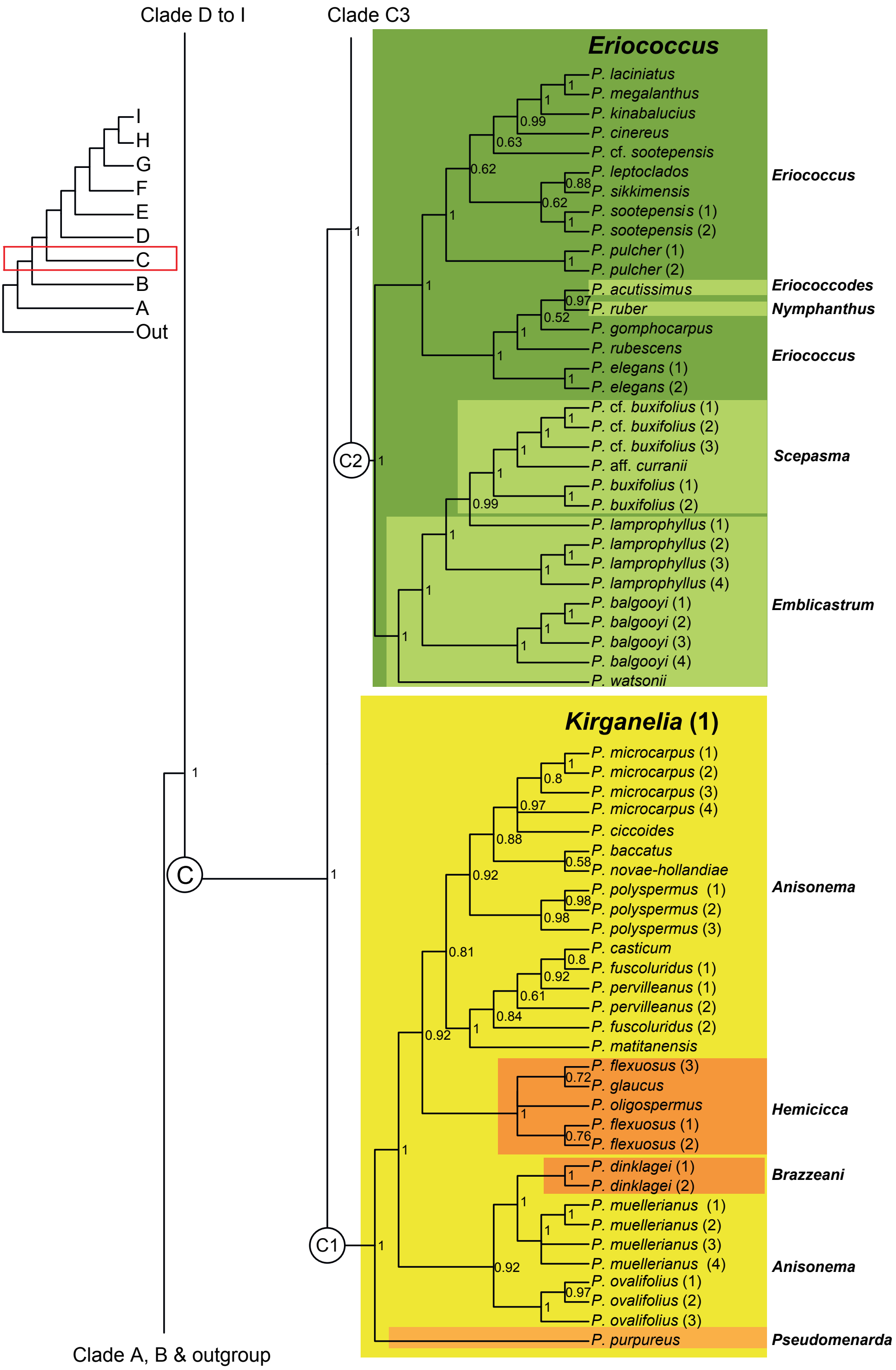


Figure 7-4. Bayesian majority rule consensus tree of the full combined nuclear (ITS and *PHYC*) and chloroplast (*accD–psaI*, *matK* and *trnS–trnG*) datasets for *Phyllanthus* and related genera, posterior probabilities (PP) are displayed at the nodes, infrageneric classification follows Bouman *et al.* (2018a); subgenera are given above colored clades, sections to the right. Outgroups and some ingroup genera are collapsed (see full tree in Suppl. Figs. 7-S10). New species are indicated with an asterisk (*).


Clade D to I
Clade C3
I
H
G
F
E
D
C
B
A
Out
Eriococcus
P. laciniatus
P. megalanthus
P. kinabalucius
P. cinereus
P. cf. sootepensis
P. leptoclados
P. sikkimensis
P. sootepensis (1)
P. sootepensis (2)
P. pulcher (1)
P. pulcher (2)
P. acutissimus
P. ruber
P. gomphocarpus
P. rubescens
P. elegans (1)
P. elegans (2)
P. cf. buxifolius (1)
P. cf. buxifolius (2)
P. cf. buxifolius (3)
P. aff. curranii
P. buxifolius (1)
P. buxifolius (2)
P. lamprophyllus (1)
P. lamprophyllus (2)
P. lamprophyllus (3)
P. lamprophyllus (4)
P. balgooyi (1)
P. balgooyi (2)
P. balgooyi (3)
P. balgooyi (4)
P. watsonii
Eriococcus
Eriococcodes
Nymphanthus
Eriococcus
Scepasma
Emblicastrum
0.99
0.63
0.62
0.88
0.62
0.97
0.52
0.99
1
C2
C
C1
Kirganelia (1)
P. microcarpus (1)
P. microcarpus (2)
P. microcarpus (3)
P. microcarpus (4)
P. ciccoides
P. baccatus
P. novae-hollandiae
P. polyspermus (1)
P. polyspermus (2)
P. polyspermus (3)
P. casticum
P. fuscoluridus (1)
P. pervilleanus (1)
P. pervilleanus (2)
P. fuscoluridus (2)
P. matitanensis
P. flexuosus (3)
P. glaucus
P. oligospermus
P. flexuosus (1)
P. flexuosus (2)
P. dinklagei (1)
P. dinklagei (2)
P. muellerianus (1)
P. muellerianus (2)
P. muellerianus (3)
P. muellerianus (4)
P. ovalifolius (1)
P. ovalifolius (2)
P. ovalifolius (3)
P. purpureus
Anisonema
Hemicicca
Brazzeani
Anisonema
Pseudomenarda
0.8
0.97
0.88
0.58
0.92
0.98
0.98
0.81
0.8
0.92
0.61
0.84
0.92
0.72
0.76
0.92
0.97
Clade A, B & outgroup

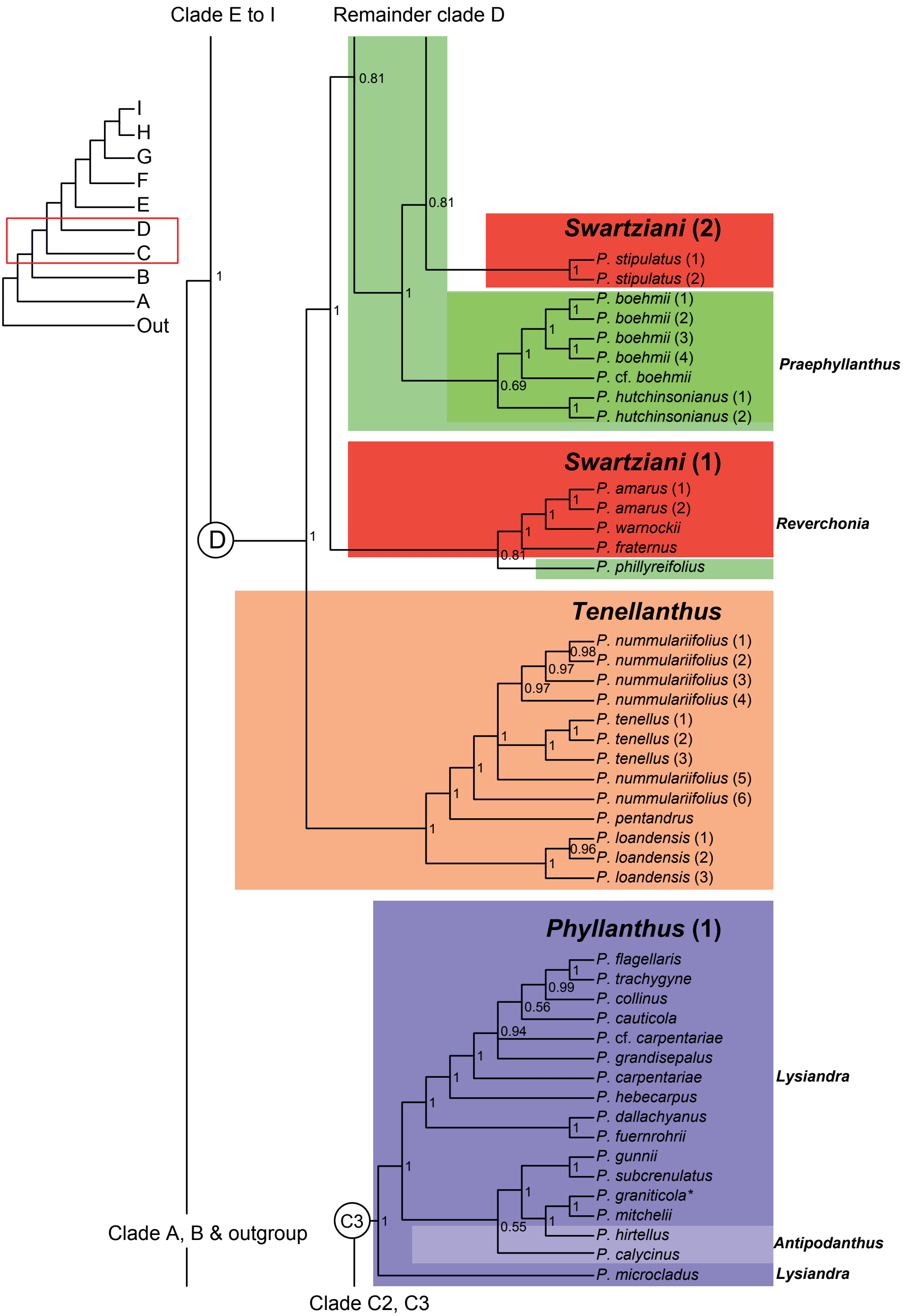
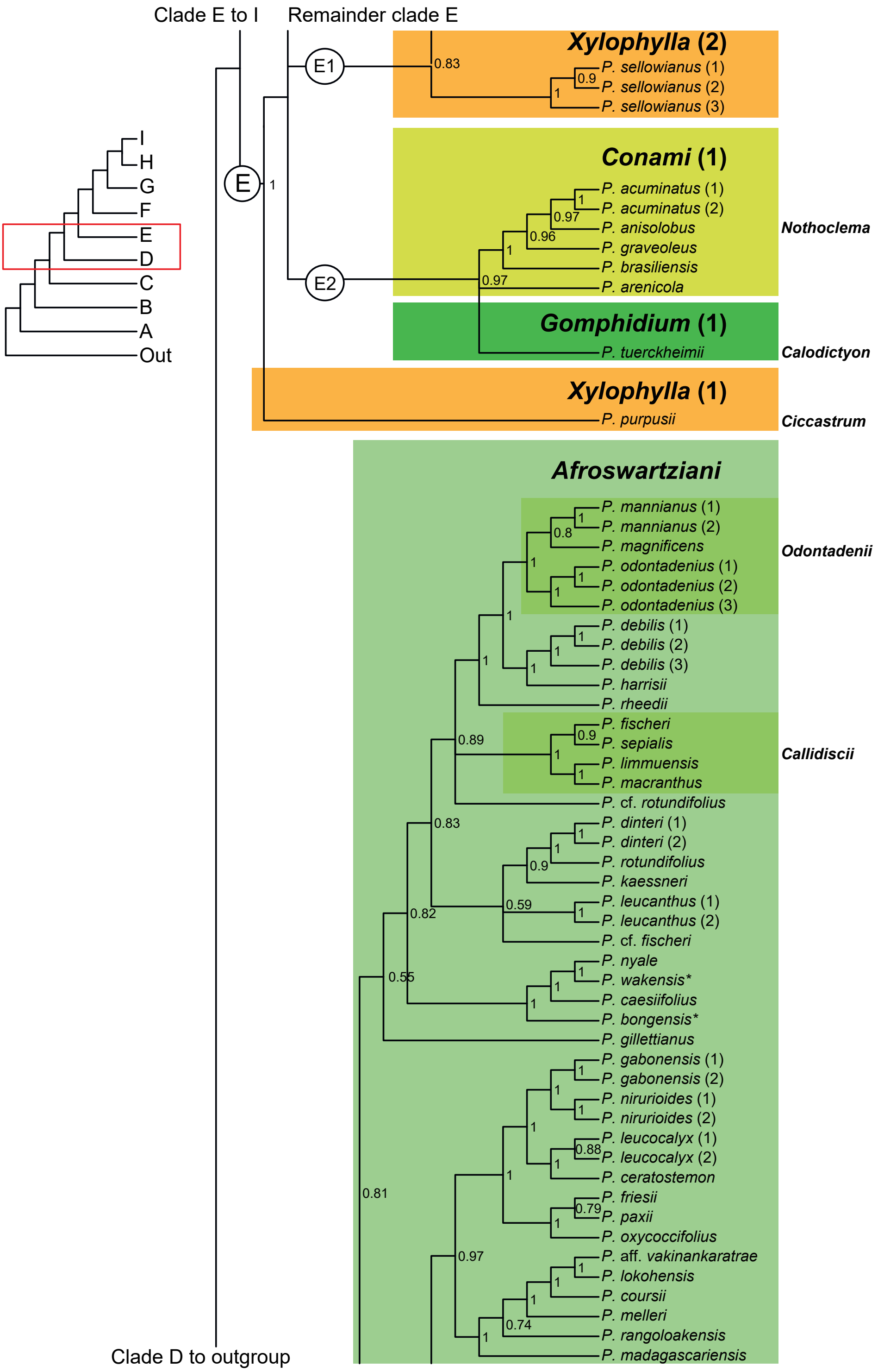


Figure 7-4. Continuation.


Clade E to I
Remainder clade E
I
H
G
F
E
D
C
B
A
Out
E
1
E1
E2
Xylophylla (2)
0.83
0.9
1
P. sellowianus (1)
P. sellowianus (2)
P. sellowianus (3)
Conami (1)
P. acuminatus (1)
P. acuminatus (2)
P. anisolobus
P. graveoleus
P. brasiliensis
P. arenicola
1
0.97
0.96
1
0.97
Nothoclema
Gomphidium (1)
P. tuerckheimii
Calodictyon
Xylophylla (1)
P. purpusii
Ciccastrum
Afroswartziani
P. mannianus (1)
P. mannianus (2)
P. magnificens
P. odontadenius (1)
P. odontadenius (2)
P. odontadenius (3)
Odontadenii
0.8
1
P. debilis (1)
P. debilis (2)
P. debilis (3)
P. harrisii
P. rheedii
P. fischeri
P. sepialis
P. limmuensis
P. macranthus
Callidiscii
0.89
0.9
P. cf. rotundifolius
P. dinteri (1)
P. dinteri (2)
P. rotundifolius
P. kaessneri
P. leucanthus (1)
P. leucanthus (2)
P. cf. fischeri
0.83
0.9
0.59
0.82
P. nyale
P. wakensis*
P. caesiifolius
P. bongensis*
P. gillettianus
0.55
P. gabonensis (1)
P. gabonensis (2)
P. nirurioides (1)
P. nirurioides (2)
P. leucocalyx (1)
P. leucocalyx (2)
P. ceratostemon
0.88
P. friesii
P. paxii
P. oxycoccifolius
0.79
0.81
P. aff. vakinankaratrae
P. lokohensis
P. coursii
P. melleri
P. rangoloakensis
P. madagascariensis
0.97
0.74
Clade D to outgroup

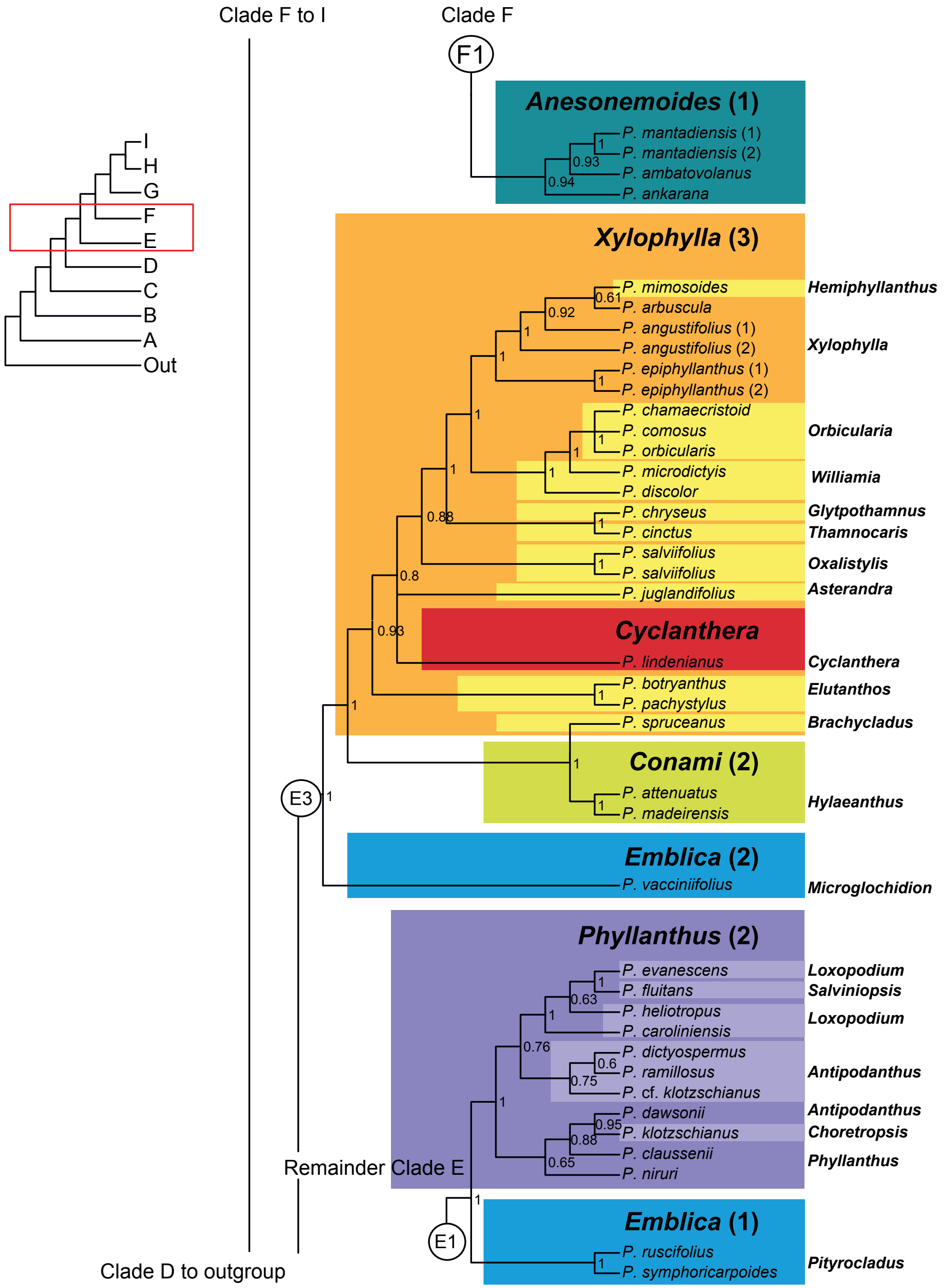
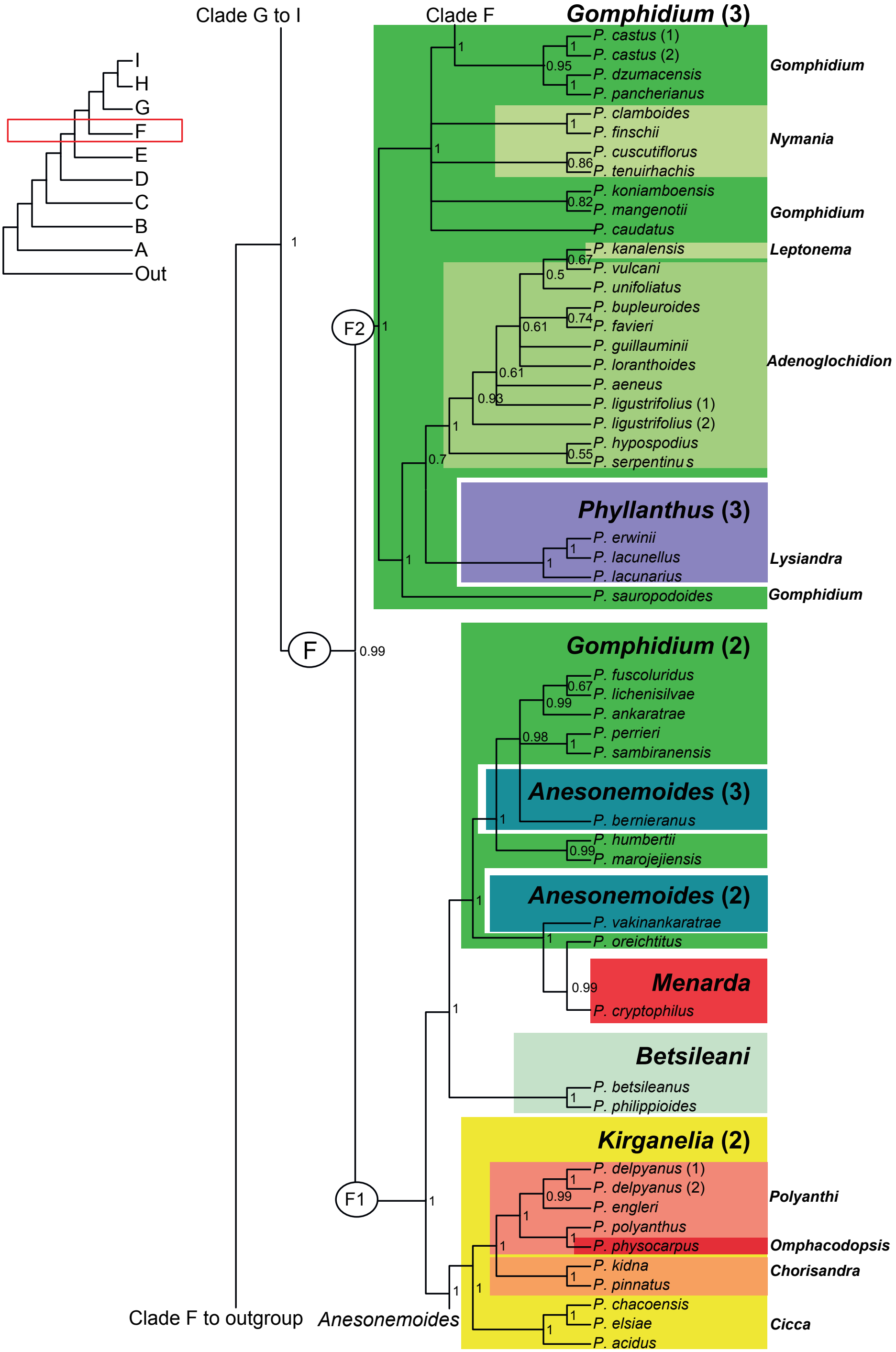


Figure 7-4. Continuation.


I
H
G
F
E
D
C
B
A
Out
Clade G to I
Clade F
Gomphidium (3)
P. castus (1)
P. castus (2)
P. dzumacensis
P. pancherianus
Gomphidium
P. clamboides
P. finschii
P. cuscutiflorus
P. tenuirhachis
Nymania
P. koniamboensis
P. mangenotii
P. caudatus
Gomphidium
P. kanalensis
Leptonema
P. vulcani
P. unifoliatus
P. bupleuroides
P. favieri
P. guillauminii
P. loranthoides
P. aeneus
P. ligustrifolius (1)
P. ligustrifolius (2)
P. hypospodius
P. serpentinus
Adenoglochidion
Phyllanthus (3)
P. erwinii
P. lacunellus
P. lacunarius
Lysiandra
P. sauropodoides
Gomphidium
F2
F
F1
Gomphidium (2)
P. fuscoluridus
P. lichenisilvae
P. ankaratrae
P. perrieri
P. sambiranensis
Anesonemoides (3)
P. bernieranus
P. humbertii
P. marojejiensis
Anesonemoides (2)
P. vakinankaratrae
P. oreichtitus
Menarda
P. cryptophilus
Betsileani
P. betsileanus
P. philippioides
Kirganelia (2)
P. delpyanus (1)
P. delpyanus (2)
P. engleri
P. polyanthus
P. physocarpus
P. kidna
P. pinnatus
P. chacoensis
P. elsiae
P. acidus
Polyanthi
Omphacodopsis
Chorisandra
Cicca
Clade F to outgroup
Anesonemoides
1
0.95
1
1
1
1
0.86
0.82
0.67
0.5
0.74
0.61
0.61
0.93
1
0.55
0.7
1
1
1
1
0.99
0.67
0.99
0.98
1
1
0.99
1
1
0.99
1
1
1
1
0.99
1
1
1
1
1
1
1
1
1

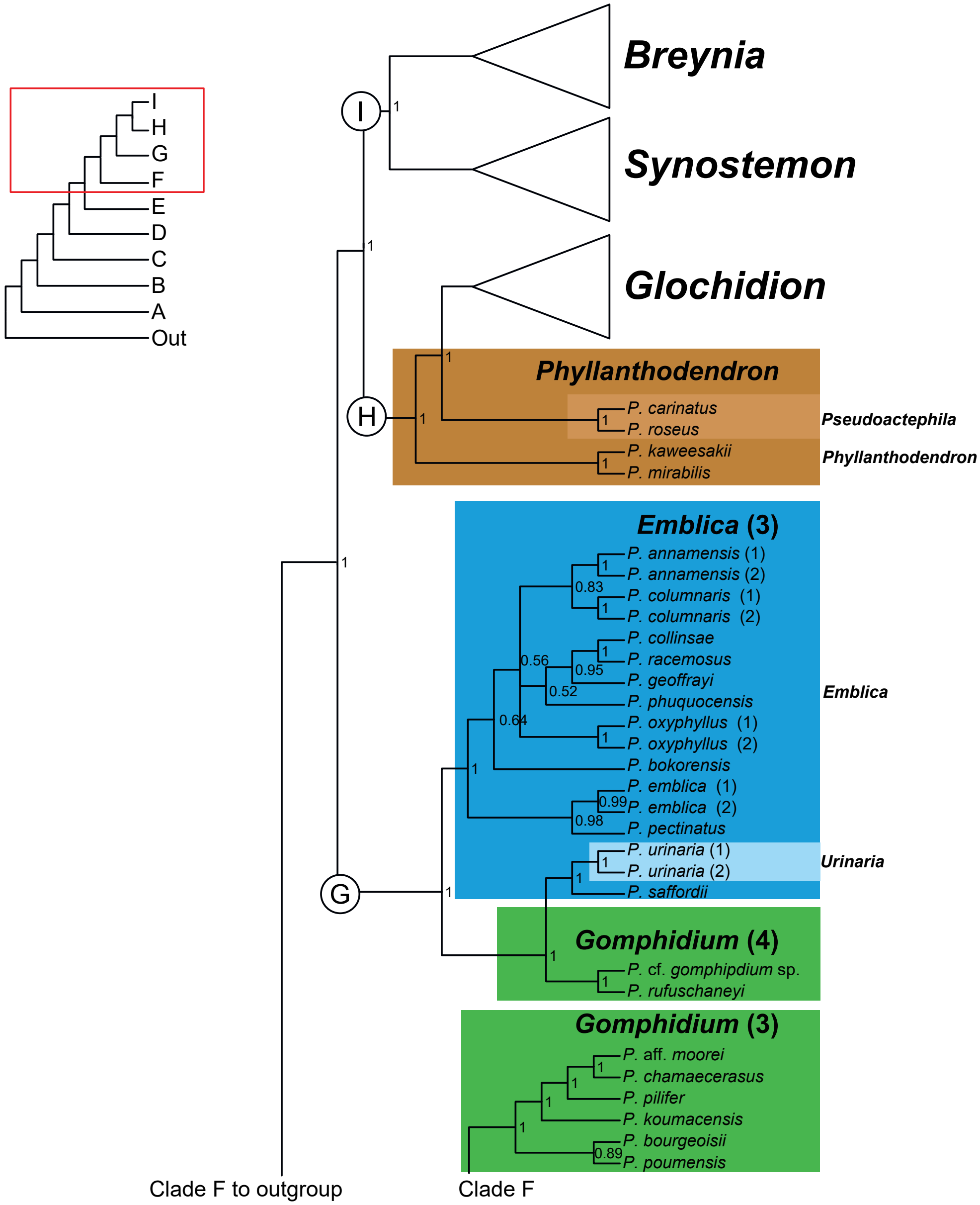


Figure 7-4. Continuation.

conservation of floral morphology appears to be a general pattern within the tribe Phyllantheae. In our phylogeny with denser taxon sampling presented here, several paraphyletic and polyphyletic subgenera and sections were discovered in various clades. These non-monophyletic groups were originally classified together on the basis of morphological ancestral commonality, but these patterns are the results of convergent evolution. Several morphological characters, such as branching type and changes in floral morphology, are indicative of various clades and are discussed below.

Non-monophyletic taxa and the subgeneric classification of Phyllanthus
Phyllanthus consists of eight clades in our phylogeny, but our results indicate the existing subgeneric classification as summarized by Bouman *et al.* (2018a) still contains several problems. Several subgenera are polyphyletic, and the paraphyly of several sections is furthermore confirmed here (Fig. 7-3). Kathriarachchi *et al.* (2006) already encountered issues in several clades, but subsequent revisions (Hoffmann*et al.* 2006; Ralimanana& Hoffmann, 2011, 2014; Ralimanana *et al.* 2013) only addressed some (most with the species from Madagascar), while others remained unresolved.

The relationships previously recovered (Kathriarachchi *et al.* 2006; Falcón *et al.* 2020) between the genera *Margaritaria*, *Flueggea*, *Heterosavia* and *Plagiocladus* are confirmed here, but the relationship of *Lingelsheimia* as sister to Flueggea and the other genera is only weakly supported (suppl. Fig. 7-S10; PP = 0.58, but see suppl. Fig. 7-S9). Six species of *Margaritaria* were included. *Margaritaria rhomboidalis* (Baill.) G.L.Webster from Madagascar is sister to all other species of the genus. Interestingly, *M. nobilis* L.f. form the Americas seems to be closely related to the Australian species *M. dubium-traceyi* Airy Shaw & B.Hyland indicating some recent long-distance dispersal. Clade A consists of *Phyllanthus maderaspatensis* of subg. *Isocladus* together with one species from North America, *P. polygonoides* Nutt. ex Spreng., and two from Africa, *P. mendoncae* Jean F.Brunel and *P. magudensis* Jean F.Brunel (currently a synonym of *P. maderaspatensis*). Ralimanana & Hoffmann (2011), based on recommendations by Kathriarachchi *et al.* (2006), removed all other species from *P.* subg. *Isocladus*, but as demonstrated here, this was premature. All species resolved here in clade A were previously classified in *P.* subg. *Isocladus* by different authors (Brunel, 1987; Webster, 2001b). *Phyllanthus* subg. *Isocladus* is here found to be larger than the monospecific definition proposed byRalimanana & Hoffmann (2011), but smaller than Webster's (1956) original conspectus (which includes former sections currently recognized as distinct subgenera).

Clade B contains 13 sampled species of *Phyllanthus* subg. *Macraea*, which are sister to four sampled species of subg. *Ceramanthus* (Fig. 7-4; PP 1.0). Three sections were included, of which *P.* subg. *Ceramanthus* sect. *Cluytopsis* Müll.Arg. was found to be sister to a clade comprising sect. *Anisolobium* Müll. Arg. and sect. *Bivia* Jean F.Brunel & Jacq.Roux. Unfortunately, we were not able to sample the type of *P.* subg. *Ceramanthus*, *P. albidiscus* (Ridl.) Airy Shaw. However, similarities in habit, branching type, flower morphology, most notably the fused connectives, rather large anthers and pantoporate pollen with macro-reticulate exine (Punt 1972; Wu *et al.* 2016), are synapomorphies for *P.* subg. *Ceramanthus*, confirming that these species belong to the same group. *Phyllanthus virgatus* G.Forst. is currently regarded as a widespread species occurring from India to the Pacific. This study includes samples from Asia and Australia, which were found to be non-monophyletic. Given the morphological variation exhibited across this complex, several other species have been proposed and some subsequently subsumed (e.g., Hunter & Bruhl, 1997; Verwijs *et al.* 2019). Denser sampling across French Polynesia and including the type region is needed to improve species delimitation. *Phyllanthus* subg. *Kirganelia* was found to be polyphyletic with species found in clades C and F (Figs. 7-3, 7-4). *Phyllanthus* sect. *Anisonema* (A.Juss.) Griseb. and sect. *Polyanthi* Jean F. Brunel were furthermore found to be paraphyletic, with sect. *Brazzeani* Jean F.Brunel & Jacq.Roux, sect. *Hemicicca* (Baill.) Müll.Arg. and sect. *Omphacodopsis* Jean F.Brunel nested within each, respectively (PP = 1.0 for both). In the phylogeny of Kathriarachchi *et al.* (2006), *P. acidus* (L.) Skeels was part of a clade separate from other species of *P.* subg. *Kirganelia*, but no subsequent transfers were made. The sole species of *P.* subg. *Kirganelia* sect. *Ciccopsis* G.L.Webster, *P. pseudocicca* Griseb., has only been collected once and has not been included in any phylogenetic study. Based on its Neotropical distribution, free stamens and inflorescence structure, it is likely related to species of clade F. *Phyllanthus* subg. *Kirganelia* (clade C) is sister to a clade that includes subg. *Eriococcus* and part of subg. *Phyllanthus*. All sections of *P.* subg. *Eriococcus* were sampled (clade C2) and sect. *Eriococcus* and sect. *Emblicastrum* were found to be paraphyletic (Fig. 7-4). *Phyllanthus* sect. *Scepasma* (Blume) Müll.Arg., sect. *Nymphanthus* (Lour.) Müll.Arg. and sect. *Eriococcodes* should be subsumed within sect. *Emblicastrum* and sect. *Eriococcus*, respectively. Clade C also consists of a clade of Australian species (clade C3), which are all currently placed in the polyphyletic *P.* subg. *Phyllanthus*. The majority of species belong to *P.* sect. *Lysiandra* (F.Muell.) G.L.Webster, originally published at subgeneric rank by Mueller (1859) with *P. subcrenulatus* F.Muell. as the type. Two species in this clade were placed by Webster (2001a, b) in *P.* subg. *Phyllanthus* sect. *Antipodanthus* G.L.Webster, together with several Neotropical species. However, the Neotropical samples are nested within the strongly supported American clade E (PP 1.0). The Australian species of *P.* sect. *Antipodanthus* should be transferred to sect. *Lysiandra* (see Webster [2020], undated manuscript "Outline of Australian *Phyllanthus*"), and clades C1, C2 and C3 should be treated at the same taxonomic rank as they are each morphologically very different (see below).

In clade D, *Phyllanthus* subg. *Tenellanthus* is sister to a clade containing subg. *Swartziani* (G.L.Webster) Ralim. & Petra Hoffm. and subg. *Afroswartziani* (PP 1.0), although there is some incongruence between the nuclear and chloroplast datasets (suppl. Figs. S1, S2; see above). In our analysis, the sampling of *P.* subg. *Swartziani* was only expanded with two extra species (*P. fraternus* G.L.Webster, *P. phillyreifolius* Poir.). The position of *P. phillyreifolius* in subg. *Swartziani* as sister to the other species (Fig. 7-4, PP 0.98) is unexpected. This species from the Mascarenes was placed in *P.* subg. *Afroswartziani* by Bouman *et al.* (2018a), which was confirmed in the nuclear dataset (suppl. Fig. 7-S1), but not in the chloroplast or total datasets (suppl. Fig. 7-S2; Figs. 7-3, 7-4). In the nuclear dataset, *P. phillyreifolius* was resolved as sister to a clade comprising Madagascan species (suppl. Fig. 7-S1, PP 1.0), which is geographically more congruent. The Neotropical species *P. stipulatus* (Raf.) G.L.Webster was resolved as part of subg *Afroswartziani*. This indicates a dispersal separate from clade E to the Neotropics (also found by Falcón *et al.* 2020: see Small Neptropical Clade). Falcón *et al.* (2020) did not include more African taxa in their phylogenetic study, but suggested to include the Neotropical *P.* subsect. *Pentaphylli* within subg. *Afroswartziani* without discussing placement in any extant section. The sampling of *P.* subg. *Afroswartziani* was greatly expanded in this study, with additional samples from sect. *Callidisci* Jean F.Brunel, sect. *Odontadenii* Jean F.Brunel and sect. *Praephyllanthus* Jean F.Brunel. Aside from these sections, there are currently no other (sub-)sectional groupings within *P.* subg. *Afroswartziani*, but our results show that this subgenus comprises two major clades. To retain previously defined sections, new groups should be defined that can be morphologically distinguished. Brunel (1987) proposed several groups, but did not validate the names. A new study of these mostly African species could result in a viable sectional classification, but we raise serious doubt whether the sections should be retained in their current form.

Clade E consists of species from the Neotropics and West Indies, but some were originally classified in mostly Palaeotropical subgenera (e.g., *Phyllanthus* subg. *Emblica* and subg. *Gomphidium*). The phylogenetic study of Falcón *et al.* (2020) also focused on this clade, and they included more species of Phyllanthus from the West Indies, but not from South America. Three main groups are distinguished in clade E, but the relationship between them is only resolved in our analysis based on the reduced dataset (suppl. Fig. 7-S8), designated as clades E1–E3. Clade E1 consists of low sprawling shrubs (*P.* subg. *Emblica* sect. *Pityrocladus*) and herbs (*P.* subg. *Phyllanthus*) and was found to be sister to a clade of *P.* subg. *Conami* sect. *Nothoclema* (E2) and a large part of subg. *Xylophylla* (E3) (Fig. 7-4, PP 1.0). *Phyllanthus* subg. *Phyllanthus*, as discussed above, is polyphyletic with other species resolved in clades C3 and F1. *Phyllanthus* subg. *Phyllanthus* in clade E contains the type, *P. niruri* L., and sect. *Antipodanthus*, sect. *Loxopodium* G.L.Webster (with sect. *Salviniopsis* Holm-Niels ex Jean F.Brunel nested within) and sect. *Choretropsis* Müll.Arg. *Phyllanthus* subg. *Conami* is retrieved in clades E2 and E3, each clade containing species of different sections (sect. *Nothoclema* and sect. *Hylaeanthus* G.L.Webster, respectively). The sister relationship of P. subg. *Conami* sect. *Hylaeanthus* and subg. *Xylophylla* sect. *Brachycladus* G.L.Webster is surprising: while they are similar in vegetative characters and staminate flowers (Webster, 2004), they differ in pollen, inflorescence structure and fruit type, possibly indicating a shift in pollinator and/or seed disperser. *Phyllanthus* subg. *Xylophylla* as defined by Webster (1958) is morphologically heterogeneous, including species with phylloclades (Fig. 7-1), non-phyllanthoid branching (sect. *Elutanthos*), and very variable floral characteristics. This might underlie the apparent polyphyly of the subgenus. The majority of species are found in clade E3, with *P. purpusii* Brandegee sister to all other species of clade E (PP 1.0). The placement of *P. sellowianus* (Klotzsch) Müll.Arg. received low support by Kathriarachchi *et al.* (2006) and Falcón *et al.* (2020) and was not confirmed here, instead being resolved as sister to other species of clade E1 (Fig. 7-4; PP 0.83). Clade E3, excluding *P. vaccinifolius* (Müll. Arg.)Müll.Arg., should be treated as subg. *Xylophylla*, but several issues need to be addressed. Falcón *et al.* (2020) did not suggest many changes to the sectional classification of *P.* subg. *Xylophylla* compared to Webster (1958). *Phyllanthus* subg. *Cyclanthera* was found both here and by Falcón *et al.* (2020) to be nested within clade E3 with a particularly long branch. Other parts of clade E (Fig. 7-4) do not differ much from clades I–IV of Falcón *et al.* (2020), but we do find that *P.* sect. *Williamia* (Baill.) Müll.Arg. is paraphyletic, while Falcón *et al.* (2020) found a weakly supported monophyletic group sister to sect. *Orbicularia* (Baill.) Griseb. Our results indicate that *P.* subg. *Xylophylla* is best to be circumscribed and restricted to clade E3 similar to Falcón *et al.* (2020), but that subg. *Cyclanthera* and subg. *Conami* sect. *Hylaeanthus* should be subsumed within it. *Phyllanthus* subg. *Xylophylla*, as defined by Webster (1958), has clypeate pollen as an apomorphy, but the apparent polyphyly and inclusion of other groups found here to be nested within it, indicates that this feature was lost independently several times. Webster (2002b) treated *P.* sect. *Microglochidion* (Müll.Arg.) Müll.Arg. and sect. *Pityrocladus* G.L.Webster within the Palaeotropical subg. *Emblica*, thereby creating a group with a disjunct distribution. The Neotropical sections are here found to be part of clades E3 and E1 and should be treated separately from other species of *P.* subg. *Emblica* (clade G). The Palaeotropical species of *P.* subg. *Emblica* (clade G) formed a monophyletic group, with the exception of *P. rufuschaneyi*, which was classified in subg. *Gomphidium* (Bouman *et al.* 2018b). This woody shrubwas retrieved as sister to the herbaceous *P.* subg. *Emblica* sect. *Urinaria* (PP 1.0) and should be transferred. *Phyllanthus* sect. *Emblica* also consists of woody shrubs and trees, and it is likely that *P. urinaria* shows a shift to herbaceous habit from a woody ancestor. If *P. rufuschaneyi* is treated in sect. *Urinaria*, then the group becomes even less distinguishable from sect. *Emblica* and both could be combined.

The species of *Phyllanthus* from Madagascar have received recent taxonomic revisions (Ralimanana & Hoffmann 2011, 2014; Ralimanana *et al.* 2013) that also updated several subgenera following the results of Kathriarachchi *et al.* (2006). Previous placements in *P.* subg. *Afroswartziani* are confirmed and they formed a single clade (PP 1.0) related to other African species. Other subgenera were here retrieved in clade F1, but not all are monophyletic. The relationship found here in clade F represents the highest contrast with the phylogeny presented by Kathriarachchi *et al.* (2006). Support for the relationships between clades H–O in their phylogeny (Kathriarachchi *et al.* 2006: fig. 3) was lower for major clades. The topological changes, found here with stronger support, probably result fromthe increased number of markers and samples used. Clade F1 here consists of several sections of *P.* subg. *Kirganelia* (discussed above) and subg. *Betsileani*, subg. *Menarda*, subg. *Anesonemoides* and part of subg. *Gomphidium*, all from Madagascar. *Phyllanthus* subg. *Menarda* is nested within a clade of Madagascan species in subg. *Gomphidium*,which is also mixed with the polyphyletic subg. *Anesonemoides*. This is a complicated group, and for the remaining species of *P.* subg. *Gomphidium* in Madagascar (Hoffmann & McPherson 2003; Ralimanana & Hoffmann 2011), a different name should be selected with some scrutiny on how many groups should be retained. *Phyllanthus* subg. *Gomphidium* was presumed to have a pantropical distribution with one species from Guatemala (*P. tuerckheimii* G.L.Webster, here found to be related to subg. Conami sect. Nothoclema; clade E2, PP 0.97), some from Madagascar (clade F1), East Malesia and New Caledonia (clades F2 and G). The majority of species in *P.* subg. *Gomphidium* were retrieved in clade F2 (PP 1.0), which contains four sections divided into two major clades all from Australia, East Malesia and NewCaledonia. *Phyllanthus* sect. *Leptonema* was found to be nested within sect. *Adenoglochidion* as sister to *P. vulcani* Guillaumin (Fig. 7-4; PP 0.67),while sect. *Nymania* was resolved as paraphyletic in the reduced dataset (suppl. Fig. 7-S8) with regard to sect. *Gomphidium*. The New Caledonian species were extensively treated by Schmid (1991), who recognized some groups, but opted not to classify them in separate subsections. The high diversity of species (>100) in *P.* subg. *Gomphidium* in Asia and the Pacific has been linked to a possible co-diversification event with its mutualistic moth pollination (Kawakita & Kato 2004a). Three herbaceous desert species from Australia, doubtfully considered as part of *P.* subg. *Phyllanthus* sect. *Lysiandra* by Bouman *et al.* (2018a), were found to be closely related to species of subg. *Gomphidium* from New Caledonia (Fig. 7-4; PP 0.7), and they should be transferred. The Australian desert species appear to represent a specialized offshoot within P. subg. *Gomphidium*, possibly driven by aridification. We confirm previously found relationships between the genera *Breynia*, *Synostemon*, *Glochidion* and *Phyllanthus* subg. *Phyllanthodendron* from Pruesapan *et al.* (2012) (here as clades H and I). *Phyllanthus* subg. *Phyllanthodendron* is paraphyletic and consists of two clades, with species of sect. *Phyllanthodendron* sister to a clade containing species of sect. *Pseudoactephila* Croizat and the genus *Glochidion* into which they should be transferred.

Morphological character evolution

Several morphological characters have been shown to be useful when distinguishing the various infrageneric taxa within *Phyllanthus*. A recent study by Gama *et al.* (2016) suggested that the two perianth whorls in *P. urinaria*—and by extension in subg. *Emblica* and the genera *Breynia* and *Glochidion*—could be distinguished as petals and sepals. However, a perianth with two whorls is also found in *P.* subg. *Macraea*, subg. *Ceramanthus* (Brunel 1987), subg. *Gomphidium* (1991) and several others. They are often indistinguishable (except in *P.* subg. *Ceramanthus* and subg. *Gomphidium*) and are perhaps better referred to as tepals (see Ralimanana

& Hoffmann 2011), but are generally treated as sepals in taxonomic treatments (Webster 1956; Chakrabarty & Balakrishnan 2018; Verwijs *et al.* 2019). Structures identified as petals also occur adjacent to the sepal whorl in other genera within Phyllanthaceae such as the genera *Actephila* Blume, *Bridelia* Willd. and *Cleistanthus* Hook.f. ex Planch. As the floral ontogeny has only been studied in a limited number of species, we cannot draw any conclusion on whether this is a true synapomorphy, as suggested by Gama *et al.* (2016). Phyllanthoid branching occurs in the majority of *Phyllanthus* species but, as found by Kathriarachchi *et al.* (2006), with several independent reversals, including desert species with a more sprawling habit and the aquatic species *P. fluitans* Benth. ex Müll.Arg. The functional "advantage" of phyllanthoid branching has not been extensively studied, although from the few studies available, it does not seem to be related to chromosome number (see Webster & Ellis 1962; Bancilhon 1971). Individual plants often exhibit sub-phyllanthoid branching within the first few nodes (Fig. 7-1E) (Webster 1956). Some species, such as those in *P.* subg. *Kirganelia* sect. *Pseudomenarda* Müll.Arg. (clade C1) and species in clade C3, retain sub-phyllanthoid branching in maturity (Brunel 1987; Telford *et al.* unpub. data).

Loss of nectar secretion in *Breynia*, *Synostemon* and *Glochidion* was interpreted as a synapomorphy for these genera, distinguishing them from *Phyllanthus* (Radcliffe-Smith 2001). The loss of the nectar disc in *Glochidion* is likely to have occurred independently as *Glochidion* is more closely related to the paraphyletic *P.* subg. *Phyllanthodendron* (Fig. 7-4). The loss of the disc has also been correlated within *Glochidion* to the presence of a pollination mutualism with moths (Kawakita & Kato, 2009), which might have led to a co-diversification of plant and pollinator. Moths were also found to pollinate flowers in *P.* subg. *Gomphidium* (clade F2) (Kawakita & Kato 2004a). A similar loss or reduction of the nectar disc is found in several species (Fig. 7-4) (Schmid, 1991; Kawakita & Kato 2004a). The nectar disc has been lost independently at least four times (clades F1, F2, H and I). Whether this loss in *P. acidus* is related to a similar pollination system requires investigation (cf. Webster 1958).

Fruit types within the genus *Phyllanthus* are sometimes characteristic of taxonomic groups. They are usually explosive schizocarpic capsules that rarely exceed 1 cm in diameter (Fig. 7-1H). Berries have evolved several times independently and are found in the genus Flueggea and within *Phyllanthus* clades C1, E3 and F1. Some species in *Breynia* produce tardily dehiscent, berry-like fruits. Berries in *Phyllanthus* are often small and hypothesized to be associated with dispersal by birds (Luo *et al.* 2011a). A marked transition in fruit morphology is found in *P.* subg. *Kirganelia* sect. *Polyanthi* and sect. *Omphacodopsis* (clade F1): species of sect. *Omphacodopsis* are characterized by inflated capsules with a very thin exocarp, whereas species in sect. *Polyanthi* have apple-like berries (Brunel 1987), which indicates a remarkable shift in dispersal strategy. Similarly, the sister relationship between *P.* subg. *Conami* sect. *Hylaeanthus* and subg. *Xylophylla* sect.

Brachycladus (clade E3) is accompanied by marked differences in fruit (capsules vs. berries) and pollen morphology (clypeate vs. porate) (Webster & Carpenter 2002; Webster 2004). The potential correlation between these morphological shifts and their ecology requires field study to understand these interesting systems of evolutionary biology.

Staminate flowers show more morphological variation between clades than pistillate flowers and are often more informative for distinguishing taxa. Pistillate flowers are usually composed of two whorls of tepals, an annular nectar disc and the 3-locular ovary with bifid stigmas (although exceptions characterize certain groups). The number of stamens is variable between the genera *Plagiocladus* to *Flueggea*, but within *Phyllanthus* and the genera nested within, the presence of mainly three stamens appears to be conserved (Fig. 7-3). *Phyllanthus* subg. *Kirganelia* (clade C) is characterized by staminate flowers with usually five stamens fused in two whorls (two outer free stamens and three inner with fused filaments). It is sister to *P.* subg. *Eriococcus* (clade C2), which has staminate flowers with four sepals arranged in a cross (Fig. 7-1J) and two fully connate stamens, and a clade C3, in which the species all have three stamens with more or less fused filaments and sometimes enlarged connectives (Telford, unpub. data). The number of pollination studies within *Phyllanthus* is expanding (e.g., Kato *et al.* 2003; Kawakita & Kato 2004a, 2009; Luo *et al.* 2011a; Kato & Kawakita 2017; Kawakita *et al.* 2019), but most have recovered variations within the mutualism with moths while the pollination system in many taxa is still unknown. In clade C, flowers of *P.* subg. *Kirganelia* (clade C1) are pollinated by mutualistic moths (Kawakita & Kato 2009), but the pollination system is not known in clades C2 and C3. With recent findings of a New World dispersal and pollination by leafflower moths (Kawakita *et al.* 2019), the question arises of how prolific this mutualism is and whether other pollination systems might depart from the standard mechanism. Unfortunately, the pollination system of other genera in tribe Phyllantheae including *Margaritaria* and *Heterosavia* remains unknown, although species in cladeAare often parasitized (not actively pollinated) by *Epicephala* moths (Kato & Kawakita 2017). Webster (1957, 1958) created many new sections for the West Indian species of *P.* subg. *Phyllanthus* and subg. *Xylophylla*, mainly because he encountered a large variation in habit and flowers: shrubs with phylloclades and flowers with three stamens and six sepals in sect. *Xylophylla* (Fig. 7-1) to low shrubs with whorled stamens, sometimes more than 10, in sect. *Orbicularia* (Webster 1958). The morphological reconstruction done by Falcón *et al.* (2020: figs. 4 & 5) shows shifts in the West Indian species in disc morphology, stamen number and branching type. With more information on the ecology of the various species, this group might be ideal to study island diversification and its causes.

Three main types of pollen are found in tribe Phyllantheae, viz. pantoporate, porate with usually three colpi, or clypeate (Webster & Carpenter 2002, 2008). Colporate pollen is found in almost all clades except in clade B, in which species of *Phyllanthus* subg. *Macraea* are characterized by clypeate pollen, whilst those of subg. *Ceramanthus* have pantoporate pollen without distinct colpi (Punt, 1972; Webster & Carpenter 2008). Clypeate pollen has evolved independently in clade E (in *P. purpusii*, which is sister to all other species of clade E), *P. sellowianus* of clade E1 and the majority of species in clade E3 (see Webster 1958; Webster & Carpenter 2008). Webster & Carpenter (2002) offered several hypotheses on the origin of clypeate pollen in Neotropical *Phyllanthus* species, but these require further study. The absence of clypeate pollen in *P.* subg. *Cyclanthera* and subg. *Conami* sect. *Hylaeanthus* indicates two independent losses of this particular pollen type in clade E3. Pollen in *P.* subg. *Cyclanthera* is characterized by a central raised pilum, which is unique among angiosperms (Webster & Carpenter 2002; Webster 2002b). Species of *P.* subg. *Cyclanthera* are herbs, and the staminate flowers have a transformed disc-like androecium (Webster 1957, 1958, 2002b), all in stark contrast to other species in clade E3, which are all woody.

New issues are identified in the infrageneric classification of *Phyllanthus*, calling for a re-assessment of the diagnostic characters previously used. Many previous classifications relied on the branching system or pollen morphology (Webster 1956, 1957, 1958; Brunel, 1987), but the independent losses of character states have obfuscated relations between various groups.

Conclusion

Resolving the paraphyly of the genus *Phyllanthus* has been the topic of discussion in several phylogenetic studies of tribe Phyllantheae (Kathriarachchi *et al.* 2006; Pruesapan *et al.* 2008, 2012; Van Welzen *et al.* 2014a). Similar situations occur in other giant genera, like *Euphorbia* L. and *Syzygium* Gaertn., which were found to be paraphyletic and subsequently combined with the genera nested within (see Bruyns *et al.* 2006; Craven & Biffin 2010; Ahmad *et al.* 2016). Seemingly, suggestions for combining taxa often provide less objections, especially if one group is already large, than doing the opposite, which would lead to recognizable units. *Breynia*, *Synostemon* and *Glochidion* are currently retained as distinct genera from *Phyllanthus* (Van Welzen *et al.* 2014a), while the clades that comprise *Phyllanthus* can be differentiated by looking at several characters. The morphological patterns and taxonomic problems highlighted here and by Kathriarachchi *et al.* (2006) support the recognition of individual clades as distinct taxa. In fact, many of the now recognized infrageneric taxa have to be redefined after our analysis as they are poly- or paraphyletic. Based on the recognizability of the monophyletic groups, redefining them as genera (which was once the case) is the best option, as, in spite of the many name changes, it provides a better reflection of the evolutionary history of *Phyllanthus* s.l. and will in the future improve identifications greatly. Instead of one giant genus, where identification is difficult and evolution is only depicted by the various subgenera, it is more sensible and worthwhile to recognize separate genera that highlight the morphological variation within the tribes. Additionally, patterns of floral convergence can be discussed in the light of separate lineages, highlighting the complex diversity of tribe Phyllantheae. Before Müller (1863, 1865, 1866) created a single large genus with many sections, several groups were treated as separate genera. The subgeneric classification proposed by Webster (1956, 1957, 1958), and expansions incorporating results from various morphological studies (notably Punt 1967, 1972, 1980, 1986, 1987), laid the foundation for discussing species relationships within this large group. Building on the framework presented by Webster (1956) and accommodating recent phylogenetic data will result in a useful evolutionary classification for tribe Phyllantheae. A number of morphological characters, such as branching, habit, floral and fruit morphology help to distinguish the groups, and we illustrate many of these characters in Figs. 7-1 and 7-3. The current study clarifies the classification uncertainty around *Phyllanthus* s.l. and provides biologists and ecologists (e.g., Kato & Kawakita 2017) with a sound and useful phylogenetic and taxonomic framework. The sampling of about 10% of Phyllanthus in Kathriarachchi *et al.* (2006) would have resulted in a larger number of genera needing to be recognized, but our current phylogeny shows good support at major nodes, and we therefore recommend dismantling *Phyllanthus* into nine genera for which names are already available. These will roughly be clades A–I (Figs. 7-3, 7-4), while retaining *Synostemon* as separate from *Breynia*, and treating *P*. subg. *Kirganelia* (clade C1), subg. *Eriococcus* (clade C2) and sect. *Lysiandra* (clade C3) as separate taxa. We will formalize these changes in a separate paper, which is in preparation.

Acknowledgments

This work was done as part of the Ph.D. research of the main author, funded by the Hortus botanicus Leiden (Leiden University) and hosted by Naturalis Biodiversity Center. Fieldwork was funded by the Alberta Mennega Stichting, which is gratefully acknowledged. The second author thanks the Leiden University Fund (LUF) for their support of the Chair Botanical Gardens and Botany of Southeast Asia. The last author thanks the Treub Maatschappij, the Society for the Advancement of Research in the Tropics, for their support of the Ornstein Chair in Tropical Plant Biogeography. The material for this project was gathered thanks to a large list of contributors. The DNA banks of Kew and Missouri Botanical Garden are gratefully acknowledged for allowing us to use some of their DNA samples. Sampling of herbarium material was done at the Naturalis Biodiversity Center (L) and the N.C.W. Beadle Herbarium (NE). Critical samples of rare tropical American species were kindly provided by Ellen Dean and Jean Shepard, Herbarium of the University of California, Davis (DAV). The following contributors are thanked for their generous help in supplying us with plant material for our DNA work: Shuichiro Tagane (Center for Asian Conservation Ecology, Kyushu University), Mark Reynders (Meise Botanical Garden), Mark Nicholson (Plants for Life), the botanical garden of Ghent, Kate Armstrong (NY), David Orr (Waimea Valley), Renyong Yu

(Naturalis Biodiversity Center), Anett Krämer (Botanischer Garten der Universität Bonn), Stig Pederson (Booderee Botanic Garden), Richard Chung (Forest Research Institute Malaysia),Marianne Lauerer (Ökologisch Botanischer Garten Universität Bayreuth), Peter Brownless (Royal Botanic Garden Edinburgh), Holly Forbes (University of California, Botanical Gardens at Berkeley), Reinout Havinga (Hortus botanicus Amsterdam), Hans Persoon (Utrecht Botanical Gardens),Michael Jay Calaramo (Northwestern University Ecotourism Park and Botanic Garden), Antony van der Ent (University of Queensland). The photos supplied by M.S. Nuraliev were made during expeditions of the Joint Russian-Vietnamese Tropical Scientific and Technological Center, which are gratefully acknowledged. Open Access funding enabled and organized by ProjektDEAL.

Appendix 7-1. GenBank accessions numbers used in phylogenetic analyses. Taxon name, origin, collector and collection number, herbarium code, accession numbers for ITS, PHYC, accD-psaI, matK, trnS-trnG. Newly generated sequences are in bold. Accessions from DNA banks of Kew and Missouri Botanical Garden are underscored. The majority of published sequences were taken from Kathriarachchi *et al.* (2006), Pruesapan *et al.* (2008, 2012) and Kawakita & Kato (2009).

Actephila excelsa (Dalzell)Müll.Arg., China, Yunnan, Xishuangbanna Tropical Botanical Garden, *Bouman & Yong RWB057* (HITBC), –,MN904188,MN915296, MN916079, –; *Antidesma bunius* (L.) Spreng., Unknown, Ghent living collection *xx0Gent19002015*, no voucher, –,MN904189, –,MN916080, –; *Breynia amoebiflora* (Airy Shaw) Welzen & Pruesapan, Thailand, Chiang Mai, *Maxwell 90-721* (L), –, –, –, EU643747, –; *B. amoebiflora* (Airy Saw) Welzen & Pruesapan, Thailand, *Kerr 19655* (P), GQ503379, GQ503437, GQ503498, –, GQ503562; *B. androgyna* (L.) Chakrab. & N.P.Balakr. (*Breynia androgyna* 1), Thailand, Chachoengsao, *Van Welzen 2006-4* (L), U623563,GQ503439,GQ503500, EU643748, GQ503564; B. androgyna (L.)Chakrab.&N.P.Balakr. (*Breynia androgyna* 3), Sri Lanka, *Kathriarachchi et al. 40* (K), AY936747, GQ503459, GQ503517, –, GQ503588; *B. asteranthos* (Airy Shaw)Welzen & Pruesapan, Thailand, Nakhon Sawan, Esser 99-13 (L), EU623565, –, GQ503501, EU643751, –; *B. bicolor* (Craib) Chakrab. & N.P.Balakr., Thailand, ChiangMai, *Esser 99-21* (L), EU623567, –, GQ503503, EU643754, –; *B. brevipes* (Müll.Arg.) Chakrab. & N.P.Blakr., Thailand, Phetchaburi, *Middleton et al. 974* (L), EU623568, –, –, EU643755, –; *B. discigera* Müll.Arg., Indonesia, N. Sumatra, *Takeuchi et al. 18873* (L), EU623550, GQ503410, –, EU643736, –; *B. discocalyx* (Welzen)Welzen & Pruesapan, Thailand, Ranong, *Beusekom & Phengklai 566* (L), GQ503387, –, –, EU643757, GQ503569; *B. disticha* J.R.Forst. & G.Forst. (*Breynia disticha* 1), Netherlands, Utrecht botanical garden, *Bouman & Verwijs RWB024* (L),MN915814,MN904191,MN915298,MN916082, MN915581; *B. disticha* J.R.Forst.& G.Forst. (*Breynia disticha* 2), Singapore, Singapore botanical garden, *Yu 63* (L), MN915815, MN904192, MN915299, MN916083, MN915582; B. fruticosa (L.) Müll.Arg., China, Hong Kong, *Bouman et al. RWB025* (L), MN915816, MN904193, MN915300, MN916084, MN915583; *B. garrettii* (Craib) Chakrab. & N.P.Balakr., China, Guinzhou, *Sino-American Guizhou Botanical Expedition 1872* (L), EU623570, GQ503444, GQ503507, EU643760, GQ503572; *B. glauca* Craib, Thailand, Nong Khai, Pooma *et al.* 2702 (L), EU623551, GQ503411, –, EU643737, GQ503532; *B. hirsuta* (Beille) Welzen & Pruesapan, Thailand, *Larsen et al. 33993* (P), GQ503391, GQ503445, –, EU643762, –; *B. kerrii* (Airy Shaw) Welzen & Pruesapan, Thailand, Tak, *Van Beusekom & Phengklai 1065* (P), EU623574, GQ503452, –, EU643764, GQ503579; *B. lanceolata* (Hook.f.) Welzen & Pruesapan, Thailand, Chanthaburi, Esser 2001-4 (L), EU623584, –, –, EU643774, –; *B. lithophila* Welzen & Pruesapan, Thailand, *Phonsena et al. 5595* (L), –, GQ503464, GQ503522, –, GQ503595; *B. macrantha* (Hassk.) Chakrab.

&N.P.Balakr.,Ausralia,Queensland, *Telford&Bruhl 13107* (L),GQ503396, –, –, –, –; *B. macrantha* (Hassk.) Chakrab.&N.P.Balakr., Thailand, Maxwell 95-1125 (L), –, –, –, MT551232, –; *B.* cf. *macrantha* (Hassk.) Chakrab. & N.P.Balakr., China, Yunnan, Xishuangbanna Tropical Botanical Garden, *Bouman & Yong RWB050* (HITBC), MN915813, MN904190, MN915297, MN916081, MN915580; B. micrasterias *Breynia micrasterias* (Airy Shaw) Welzen & Pruesapan, Malaysia, Sarawak, *Erwin & Chai S 27479* (L), EU623578, GQ503455, –, EU643768, GQ503582; "*B. novoguineensis*" msc. name, sp. nov., Indonesia, Papua, *Baker et al. 37* (L), EU623549, GQ503409, GQ503472, –, GQ503530; *B. oblongifolia* (Müll.Arg.) Müll. Arg., Australia, *Forster 32745* (NE), GQ503355, GQ503414, GQ503475, –, GQ503534; *B. orbicularis* (Craib) Welzen & Pruesapan, Laos, Vientiane, *Soejarto & Southavong 10792* (L), EU623580, GQ503456, GQ503513, AY936645, GQ503584; *B. poomae* (Welzen & Chayam.) Welzen & Pruesapan, Thailand, Chiang Rai, *Phonsena et al. 5245* (L), EU623582, GQ503457, GQ503515, EU643771, GQ503586; *B. repens* Welzen & Pruesapan, Thailand, *Middleton et al. 2287* (L), GQ503385, –, –, –, GQ503566; *B. retusa* (Dennst.)Alston, Sri Lanka, *Kathriarachchi et al. 43* (K), –, –, –,AY936565, –; *B. retusa* (Dennst.)Alston, Laos,Vientiane, *Soejarto & Southavong 10783* (L), GQ503358, GQ503417, GQ503477, –, GQ503536; *B. rostrata* Merr., China, Yunnan, Xishuangbanna Tropical Botanical Garden, *Bouman & Yong RWB055* (HITBC), MN915817, MN904194, MN915301, MN916086, MN915585; *B. similis* (Craib) Welzen & Pruesapan (*Breynia similis* 1), Chiang Mai, Thailand, Larsen *et al.* 46639 (L), GQ503399, GQ503462, GQ503520, EU643778, GQ503592; B. similis (Craib) Welzen & Pruesapan (Breynia similis 2), China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB054 (HITBC), MN915818, MN904195, MN915302, MN916085, MN915584; B. spatulifolia (Beille) Welzen & Pruesapan, USA, Honolulu, Wong s.n. (L), EU623588, –, GQ503523, AY936647, GQ503596; B. stipitata Müll. Arg., UK, RBG Kew, living collection from Australia, Queensland, Chase 14461 (K), –, –, –, AY552422, –; B. stipitata Müll.Arg., Australia, Bruhl 2478 (NE), GQ503359, GQ503418, GQ503478, –, GQ503537; B. thorelii (Beille) Welzen & Pruesapan, Thailand, Chiang Mai, Van Welzen 2006-1 (L), EU623590, GQ503468, GQ503526, EU643782, GQ503600; B. thyrsiflora (Welzen) Welzen & Pruesapan, Thailand, Kanchanaburi, Kostermans 765 (L), EU623591, GQ503469, GQ503527, EU643783, GQ503601; B. vestita Warb., Indonesia, Papua, Barker & Beaman 70 (L), EU623553, GQ503419, GQ503480, EU643738, GQ503540; B. villosa (Blanco)Welzen & Pruesapan, Thailand, Phengklai *et al.* 12122 (BKF), EU623593, –, –, EU643786, –; B. vitis-idea (Burm.f.) C.E.C.Fisch. (Breynia vitis-idea 1), Vietnam, Tagane *et al.* V388 (L), MN915819, MN904184, MN915303, MN916087, –; B. vitis-idea (Burm.f.) C.E.C.Fisch. (Breynia vitisidea 2), Vietnam, Tagane *et al.* V404 (L), MN915820, MN904185,MN915304,MN916088, MN915586; B. vitis-idea (Burm.f.) C.E.C.Fisch. (Breynia vitis-idea 3), Philippines, Majaducon 5676 (L), MN915821,MN904186, MN915305,MN916089, –; B. vitis-idea (Burm.f.) C.E.C.Fisch. (Breynia vitis-idea 4), Singapore, Singapore botanical garden, Yu 157 (L), MN915822, MN904187, MN915306, MN916090, MN915587; Bridelia tomentosa Blume, China, Yunnan, Xishuangbanna TropicalBotanicalGarden, Bouman&Yong RWB063 (HITBC), –,MN904196,MN915307,MN916359, –; Flueggea virosa (Roxb. ex Willd.) Royle (Flueggea virosa 1), China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yunhong RWB068 (HITBC), MN915824, MN904197, MN915308, MN916091, –; Flueggea virosa (Roxb. ex Willd.) Royle (Flueggea virosa 2), Australia, Mitchel 2890 (BRI), MN915823, –, –, MN916104, –; Flueggea virosa (Roxb. ex Willd.) Royle (Flueggea virosa 3), Indonesia, Chase 2104 (K), –, –, –, AY552426, –; Flueggea virosa (Roxb. ex Willd.) Royle (Flueggea virosa 3), Thailand, Larsen *et al.* 45328 (L), –, GQ503420, GQ503481, –, –; Flueggea virosa (Roxb. ex Willd.) Royle (Flueggea virosa 4), Singapore, Singapore botanical garden, Yu 64 (L), MN915825, MN904198, –, MN916092, MN915588; Glochidion benthamianum Domin, Australia, Bruhl 1026 (NE), GQ503363, –, GQ503482, –, GQ503541; G. ellipticum Wight (Glochidion ellipticum 1), China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB058 (HITBC), MN915826, MN904199, MN915310, MN916093, MN915589; G. ellipticum Wight (Glochidion ellipticum 2), China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB061 (HITBC),MN915827,MN904200,MN915311,MN916094,MN915590; G. ellipticum Wight (Glochidion ellipticum 3), China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB062 (HITBC), MN915829, MN904202, MN915309, MN916096, MN915591; G. eriocarpum Champ. ex Benth., China, Hong Kong, Bouman *et al.* RWB027 (L), MN915828, MN904201, –, MN916095, MN915592; G. ferdinandi (Müll.Arg.) Pax & K.Hoffm., Australia, Bruhl 2457 (NE), GQ503366, GQ503421, GQ503484, –, GQ503543; G. harveyanum Domin, Australia, Bruhl 2527 (NE), GQ503368, GQ503423, GQ503486, –, GQ503545; G. lanceolarium (Roxb.) Voigt, China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB064 (HITBC),MN915830,MN904203,MN915312,MN916097,MN915593; G. lanceolatum Hayata, New Caledonia, Kawakita 116 (KYO), AY525687, FJ235327, –, FJ235235, –; G. lobocarpum (Benth.) F.M.Bailey, Australia, Bruhl 1146 (NE), GQ503371, GQ503424, GQ503488, –, GQ503548; G. philippicum (Cav.) C.B.Rob., Australia, Forster 29379 (NE), GQ503373, GQ503426, GQ503490, –, GQ503550; G. puberumGlochidion puberum (L.) Hutch., China, Guizhou, Chase 11460 (K), AY936659, –, –, AY552428, –; G. sphaerogynum (Müll.Arg.) Kurz (Glochidion sphaerogynum 1), Thailand, Van der Scheur 128 (L),MN915831, MN904204,MN915313,MN916280,MN915594; G. sphaerogynum (Müll.Arg.) Kurz (Glochidion sphaerogynum 2), Thailand, Van Welzen 2003-21 (L), EU623555, GQ503427, –, EU643740, GQ503551; G. wrightii Benth., China, Hong Kong, Bouman & Liu RWB032 (L), MN915832, MN904205, MN915314, MN916098, MN915595; Heterosavia bahamensis (Britton) Petra Hoffm., USA, Fairchild tropical garden (cultivated), Wurdack D048 (US), AY936749, AY830381, –, AY830284, –; Leptopus chinensis (Bunge) Pojark., UK, Edinburgh Botanical garden (cultivated), Brownless s.n. (L), MN915833, MN904206, MN915315, MN916099, –; Lingelsheimia sp., Madagascar, Rabenantoandro *et al.* 1115 (MO), AY936662, AY830375, –, AY830272, –; Margaritaria anomala (Baill.) Fosberg, Madagascar, Ramison 413 (MO),MN915834, –, –,MN916100, –; M. discoidea (Baill.) G.L.Webster (Margaritaria discoidea 1), Kenya, Nicholson 1 (L), –,MN904208, MN915317,MN916102, –; M. discoidea (Baill.) G.L.Webster (Margaritaria discoidea 1), Kenya, Nicholson s.n. (L), –, MN904207, MN915316, MN916101, –; M. discoidea (Baill.) G.L. Webster (Margaritaria sp. Uganda), Uganda, Nicholson 3a (L), MN915835, MN904211, MN915320, MN916107, MN915597; M. dubiumtraceyi Airy Shaw & B. Hyland, Australia, Forster 29387 (BRI), –, –, MN935815, MN916103, –; M. indica (Dalzell) Airy Shaw, Singapore, Singapore botanical garden, Orr 80532, no voucher, –, MN904209, MN915318, MN916105, –; M. nobilis L.f., Puerto Rico, Orr 875422, no voucher, –, MN904210, MN915319, MN916106, MN915596; M. rhomboidalis (Baill.) G.L.Webster, Madagascar, Rabenantoandro *et al.* 656 (K), AY936665, –, –, AY936571, –; Notoleptopus decaisnei (Benth.) Vorontsov. & Petra Hoffm., Australia, Evans 3222 (K), AM745836, –, –,AM745833, –;N. decaisnei (Benth.) Vorontsov.&PetraHoffm.,Australia, Fraser 267 (L), –, GQ503431, GQ503491, –, GQ503555; Phyllanthus acidus (L.) Skeels, Thailand, VanWelzen 2003-14 (L),MN915836, GQ503432,GQ503492,MN916108, GQ503556; P. acuminatus Vahl (Phyllanthus acuminatus 1),Venezuela, Breteler 4238(WAG),MN915837,MN904212,MN915321, MN916109,MN915598; P. acuminatus Vahl (Phyllanthus acuminatus 2),Guatemala, Wallnöfer 6031 (U), MN915838, MN904213, MN915322, MN916110, MN915599; P. acutissimus Miq., Thailand, TRP-5004102 (BK), AB550090, –, –, –, –; P. aeneus Baill., New Caledonia, Kawakita 272 (KYO), –, FJ235352, –, FJ235260, –; P. amarus Schumach. & Thonner (Phyllanthus amarus 1), Thailand, Van Welzen 2006-5 (L), EU623557, GQ503433, GQ503493, EU643742, GQ503557; P. amarus Schumach. & Thonner (Phyllanthus amarus 2), Gabon, Wieringa 8189 (WAG), MN915847, MN904217, MN915331, MN916114, –; P. ambatovolanus Leandri, Madagascar, Randriamampionona *et al.* 51 (K), MN915848, MN904218,MN915332,MN916115, MN915605; P. angustifolius (Sw.) Sw., Germany, Bayreuth botanical garden living collection, Lauerer 091479, no voucher, MN915849, MN904219, MN915333, MN916116, MN915606; P. anisolobus Müll.Arg., Costa Rica, Liesner 14363 (U), MN915850, MN904220, MN915334, MN916117, MN915607; P. ankarana Leandri, Madagascar, Ralimanana *et al.* 663 (K), MN915851, MN904221, MN915335, MN916118, MN915608; P. ankaratrae (Leandri) Petra Hoffm. & McPherson, Madagascar, Rakotonasolo & Zachary 802 (K), MN915852, MN904222, MN915336, MN916119, MN915609; P. annamensis Beille (Phyllanthus annamensis 1), Vietnam, Yahara *et al.* V3843 (L), MN915853, MN904223, MN915337, MN916120, –; P. annamensis Beille (Phyllanthus annamensis 2), Vietnam, Tagane *et al.* V3863 (L),

MN915854, MN904224, MN915338, MN916121, –; P. arbuscula (Sw.) J.F.Gmel., Belgium, Meisse living collection, Reynders 19074182 (L),MN915855,MN904226,MN915339,MN916123,MN915610; P. arenicola Casar., Brazil, Maas & Carauta s.n. (U), –, MN905071, MN915340, MN916124, MN915611; P. attenuatus Miq., Venezuela, Breteler 4696 (WAG), MN915856, MN904304, MN915341, MN916125, MN915612; P. baccatus F.Muell. ex Benth., Australia, Mitchell PRP1514 (NE), –, –, MN915342, MN916126, MN915613; P. balgooyi Petra Hoffm. et a.J.M.Baker (Phyllanthus balgooyi 1),Malaysia, Sabah, Van der Ent, no voucher,MN915857, MN904227,MN915343,MN916300, MN915614; P. balgooyi Petra Hoffm. et a.J.M.Baker (Phyllanthus balgooyi 2), Malaysia, Sabah, Yu 192 (L),MN915858, MN904228, MN915344, MN916301, MN915615; P. balgooyi Petra Hoffm. et a.J.M.Baker (Phyllanthus balgooyi 3), Philippines, Yu 259 (L), MN915859, MN904229, MN915345, MN916324, MN915616; P. balgooyi Petra Hoffm. et a.J.M.Baker (Phyllanthus balgooyi 4), Philippines, Agoo 5700 (L), MN915860, MN904230, MN915346, MN916325, MN915617; P. beckleri Müll.Arg., Australia, Hosking 2680 (NE), MN915861, MN904231, MN915347, MN916127, MN915618; P. bernieranus Baill. ex Müll.Arg., Madagascar, Phillipson 5373 (K), MN915862, MN904232, MN915348, MN916128, MN915619; P. betsileanus Leandri, Madagascar, Labat 2402 (K), MN915863, MN904233, MN915349, MN916360, MN915620; P. boehmii Pax var. boehmii (Phyllanthus boehmii 1), Tanzania, Gereau 5007 (WAG), MN915864, MN904254,MN915350,MN916302,MN915621; P. boehmii Pax var. boehmii (Phyllanthus boehmii 2),Kenya,Wieringa 8841 (WAG),MN915865,MN904234, MN915351,MN916129,MN915622; P. boehmii Pax var. humilis Radcl.-Sm. (Phyllanthus boehmii 3), Tanzania, Bidgood 6838 (WAG),MN915866,MN904235, MN915352,MN916130, MN915623; P. boehmii Pax var. humilis Radcl.-Sm. (Phyllanthus boehmii 4), Zaire, Lisowski 13765 (WAG), MN915867, MN904303, MN915353, MN916131, MN915624; P. cf. boehmii Pax, Ethiopia, Friis 13159 (WAG), MN915883, MN904249, MN915371, MN916143, MN915635; P. bokorensis Tagane, Cambodia, Toyama *et al.* 1740 (FU), –, –, MN915354, MN916132, –; “P. bongensis” msc. name, sp. nov., Ethiopia, de Wilde 7858 (WAG), MN915868, MN904305, MN915355, MN916284, –; P. botryanthus Müll.Arg., Curacao, de Wilde 31 (WAG), MN915869, MN904255, MN915356, MN916133, MN915625; P. bourgeoisii Baill., New caledonia, McMillan 5201 (WAG), MN915870, MN905064, MN915357, MN916134, –; P. brasiliensis (Aubl.) Poir., Peru, Loreto, Pongo de Cainarachi, Ule 6408 (L),MN915871,MN904236, MN915358,MN916135, MN915626; P. bupleuroides Baill., New Caledonia, McPherson 18692 (MO),MN915872,MN904237,MN915359,MN916136, –; P. buxifolius (Blume)Müll.Arg. (Phyllanthus buxifolius 1), Singapore, Singapore botanical garden, Yu 163 (L), MN915873, MN904240, MN915360,MN916326, MN915627; P. buxifolius (Blume) Müll.Arg. (Phyllanthus buxifolius 2), Singapore, Singapore botanical garden, Yu 167 (L), MN915874, MN904241, MN915361, MN916285, MN915628; P. cf. buxifolius (Blume) Müll.Arg. (Phyllanthus cf.

buxifolius 1), Philippines, Agoo 5659 (L), MN915884, MN904238, MN915372, MN916286, MN915636; P. cf. buxifolius (Blume) Müll.Arg. (Phyllanthus cf. buxifolius 2), Philippines, Agoo 5683 (L), MN915885, MN905070, MN915373, MN916287, MN915637; P. cf. buxifolius (Blume) Müll.Arg. (Phyllanthus cf. buxifolius 3), Philippines, Agoo 5738 (L), MN915886, MN904239, MN915374, MN916328, MN915638; P. caesiifolius Petra Hoffm. & Cheek, Cameroon, Cheek 10376 (WAG), MN915875, MN904242, MN915362, MN916137, MN915629; P. calycinus Labill., Australia, Chase MWC 2163 (K), AY936674, AY579869, –, AY552446, –; P. carinatus Beille, Cambodia, Toyama *et al.* 3212 (FU), –, MN904243, MN915363, MN916138, –; P. caroliniensis Walter, Suriname, Groenendijk 55 (WAG), MN915876, –, MN915364, MN916139, MN915630; P. carpentariae Müll. Arg., Australia, Clarkson & Neldner 8410 (L), MN915877, MN905063, MN915365, MN916140, MN915631; P. cf. carpentariae Müll.Arg., Australia, Hyland 8033 (L), MN915888, MN904256, MN915376, MN916147, MN915639; P. casticum P. Willemet, Madagascar, Wolhauser SW60172 (WAG), MN915878, MN904244, MN915366, MN916141, –; P. castus S.Moore (Phyllanthus castus 1),NewCaledonia, Mackee 16581 (L),MN915879,MN904246,MN915367,MN916327,MN915632; P. castus S.Moore (Phyllanthus castus 2), New Caledonia, McPherson 19255 (MO), MN915880, MN904245, MN915368, MN916304, –; P. caudatus Müll.Arg., New Caledonia, Kawakita 278 (KYO), –, FJ235351, –, FJ235259, –; P. cauticola J.T.Hunter & J.J.Bruhl, Australia, Mitchell 837 (NE), MN915881, MN904247, MN915369, MN916303, MN915633; P. ceratostemon Brenan, Tanzania, Bidgood 6776 (WAG), MN915882, MN904248, MN915370, MN916142, MN915634; P. chacoensisMorong, Paraguay, Krapovickas *et al.* 45628 (K),AY936677, –, –, AY936582, –; P. chamaecerasus Baill.,NewCaledonia,Munzinger&McPherson 573 (MO), AY936678, –, –, AY936583, –; P. chamaecristoid Urb., Cuba, van Ee *et al.* 404 (K), AY936679, –, –, AY936584, –; P. chrysanthus Baill., New Caledonia, Munzinger & McPherson 796 (MO), AY936680, –, –, AY936585, –; P. chryseus Howard, Cuba, Van Ee *et al.* 387 (K), AY936681, MN904257, MN915379, AY936586, MN915644; P. ciccoides Müll. Arg, Australia, Paijmans 2876 (DAV), MN915891, –, –, MN916150, –; P. cinctus Urb., Cuba, Ekman 19166 (K), MN915892, MN904258, MN915380, MN916151, MN915645; P. cinereus Müll.Arg., Sri Lanka, Kathriarachchi *et al.* 66 (K), AY936682, MN904259, MN915381, AY936587, –; P. clamboides (F.Muell.) Diels, Australia, Forster 26376 (L), MN915893, MN904260, MN915382, MN916152, MN915646; P. claussenii Müll.Arg., Brazil, Minas Gerais, Hatschbach 64117 (U), MN915894, MN904261, MN915383, MN916153, MN915647; P. cochinchinensis Spreng., China, Hong Kong, Bouman *et al.* RWB026 (L),MN915895,MN904262,MN915384,MN916154,MN915648; P. aff. cochinchinensis Spreng. (Phyllanthus aff. cochinchinensis 1), China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB052 (HITBC), MN915840, MN904250,MN915324,MN916144, MN915601; P. aff. cochinchinensis Spreng. (Phyllanthus aff. cochinchinensis 2), China, Yunnan, Xishuangbanna Tropical

Botanical Garden, Bouman & Yong RWB065 (HITBC), MN915841, MN904251, MN915325, MN916145, MN915602; P. aff. cochinchinensis Spreng. (Phyllanthus aff. cochinchinensis 3), China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB060 (HITBC), MN915842, MN904252, MN915326, MN916146, MN915603; P. collinsae Craib, Thailand, Middleton 3302 (L), MN915896, MN904263, MN915385, MN916155, MN915649; P. collinus Domin, Australia, Telford & Bruhl 13119 (L), –,MN904264, MN915386,MN916156, MN915650; P. columnaris Müll.Arg. (Phyllanthus columnaris 1), Myanmar, Fujikawa *et al.* 095327 (L), –, MN904302, MN915387, MN916157, MN915651; P. columnaris Müll.Arg. (Phyllanthus columnaris 2), Myanmar, Funakoshi *et al.* 085264 (L),MN915897, –,MN915388,MN916283,MN915652; P. aff. columnaris Müll.Arg. (Phyllanthus aff. columnaris 1), Thailand,Middleton 1715 (L),MN915843, MN904215,MN915327,MN916112,MN915600; P. aff. columnaris Müll.Arg. (Phyllanthus aff. columnaris 2), Thailand, Tagane *et al.* T570 (L), MN915844, MN904216, MN915328, MN916113, –; P. comosus Urb., Cuba, Gutierrez *et al.* 81777 (WIS), AY936685, –, –, AY936590, –; P. coursii Leandri, Madagascar, Razafindrahaja 184 (MO),MN915898, MN904266, MN915389,MN916329, –; P. cryptophilus (Comm. ex A.Juss.) Müll.Arg., Madagascar, Dumetz 593 (WAG), MN915899, MN904265, MN915390, MN916358, MN915653; P. aff. curranii C.B.Rob., Philippines, Yu 261 (L), MN915900, MN904267, MN915391, MN916158, MN915604; P. cuscutiflorus S.Moore, Singapore, Singapore botanical garden, Yu 61 (L), MN915901, MN904268, MN915392, MN916299, MN915654; P. dallachyanus Benth., Australia, Forster 32938 (NE), –, –, MN915393, MN916298, MN915655; P. dawsonii Steyerm., Brazil, da Silva 2073 (DAV),MN915902, –, –,MN916159, –; P. debilis J.G.Klein exWilld. (Phyllanthus debilis 1),China,HongKongUniversity campus, Bouman &LiuRWB037 (L),MN915903,MN904269,MN915394,MN916330, MN915656; P. debilis J.G.Klein exWilld. (Phyllanthus debilis 2), China, Hong Kong University campus, Bouman RWB071 (L),MN915904, MN904270, MN915395,MN916331, MN915657; P. debilis J.G.Klein exWilld. (Phyllanthus debilis 3), Philippines, Kamarudim et apok s.n. (L),MN915905,MN904271,MN915396,MN916332, MN915658; P. delpyanus Hutch. (Phyllanthus delpyanus 1), Republic of the Congo, Kami *et al.* 1215 (WAG),MN915906, –,MN915397,MN916161,MN915659; P. delpyanus Hutch. (Phyllanthus delpyanus 2), Republic of the Congo, M'Boungou 659 (WAG), –, MN904272, MN915398, MN916160, –; P. dictyospermus Müll.Arg., Brazil, Santos 5712 (DAV), MN915907, –, –, MN916162, –; P. dinklagei Pax (Phyllanthus dinklagei 1), Gabon, Bissiengou (WAG), MN915908, MN904273, MN915399, MN916333, MN915660; P. dinklagei Pax (Phyllanthus dinklagei 2), Gabon, Maas 9993 (WAG),MN915909, MN904274,MN915400, MN916334,MN915661; P. dinteri Pax (Phyllanthus dinteri 2), Namibia, Damaraland,Wilhemstal, Dinter 213 (WAG), MN915910, –, MN915401, MN916335, MN915662; P. dinteri Pax (Phyllanthus dinteri 1), Namibia, Oliver 6543 (WAG), MN915911,MN905069,MN915402, MN916336, MN915663; P. discolor Poepp. ex Spreng, Cuba, Berazain *et al.* 71878 (K), AY936688, MN904275, MN915403,AY936593,MN915664; P. distichusHook.&Arn., USA, Hawai'i,Harold st. John 17.985 (L) (L),MN915912,MN904276,MN915404,MN916163, MN915665; P. dzumacensis M.Schmid,NewCaledonia, Jaffre 2412 (L),MN915913,MN905065,MN915405,MN916164,MN915666; P. elegans Wall. exMüll. Arg. (Phyllanthus elegans 1), Vietnam, Yahara *et al.* V3499 (L),MN915914, –,MN915406,MN916165, –; P. elegansWall. exMüll.Arg. (Phyllanthus elegans 2), Vietnam, Yahara *et al.* V5597 (L), MN915915, MN904277, MN915407, MN916166, –; P. elsiae Urb., Venezuela, Davidse & Gonzalez 13359 (L), MN915916, MN904278, MN915408, MN916337, MN915667; P. emblica L. (Phyllanthus emblica 1), Myanmar, Makino banical garden expedition(2015) 103008 (MBK), MN915917, MN904279, MN915409, MN916167, MN915668; P. emblica L. (Phyllanthus emblica 2), Thailand, Phu Kae botanical garden, Van Welzen 2003-11 (L), GQ503378, GQ503434, GQ503494, EU643743, GQ503558; P. engleri Pax, Tanzania, Mwangulango 1138 (WAG), –, MN905066, MN915410, MN916168, MN915669; P. epiphyllanthus L. (Phyllanthus epiP. 1), Germany, Bayreuth botanical garden, living collection, Lauerer 080405, no voucher, MN915918, MN904225, MN915411, MN916122, MN915670; P. epiphyllanthus L. (Phyllanthus epiP. 2), Belgium, Meisse, living collection, Reynders IPEN: XX-0-BR-19840633 (L), MN915919, MN904280, MN915412, MN916169, MN915671; P. erwinii J.T.Hunter & J.J.Bruhl, Australia, Mitchell PRP1456 (NE), MN915920, MN904281, MN915413, MN916338, –; P. evanescens Brandegee, Nicaragua, Stevens 32461 (MO), MN915921, MN904282, MN915414, MN916339, –; P. exilis S.Moore, Australia, Hunter *et al.* 1528 (L), MN915922, MN904283, –, MN916362, MN915672; P. favieri M.Schmid, New Caledonia, McPherson & Munzinger 18028 (MO), AY936690, –, –, AY936596, –; P. filicaulis Benth., Australia, Telford 13516 (NE), MN915923, MN904284, MN915415, MN916170, MN915673; P. finschii K.Schum., Papua New Guinea, Takeuchi et ama 15603 (L), MN915924, MN904285, MN915416, MN916171, MN915674; P. fischeri Pax, Tanzania, Gereau 1996 (WAG), MN915925, MN904286, MN915417, –, MN915675; P. cf. fischeri Pax, Ethiopia, de Wilde 4391 (WAG), MN915887, MN905067, MN915375, MN916343, MN915725; P. flagellaris Benth., Australia, Fryxell & Craven (L), MN915926, MN904287, MN915418, MN916307, MN915676; P. flexuosus (Siebold & Zucc.) Müll.Arg. (Phyllanthus flexuosus 1), China, Chow 132 (L), MN915927, MN904289, MN915419, MN916173, MN915677; P. flexuosus (Siebold & Zucc.) Müll.Arg. (Phyllanthus flexuosus 2), USA, Berkely, Cultivated, Mcnamara 162 Living collection Berkeley, no voucher,MN915928,MN904290,MN915420,MN916174,MN915678; P. flexuosus (Siebold&Zucc.)Müll.Arg. (Phyllanthus flexuosus 3), Myanmar, Aung *et al.* 092433 (MBK), MN915929, MN904288, MN915421, MN916172, MN915679; P. fluitans Benth. ex Müll.Arg., Germany, Cultivated Botanical garden Bonn, Krämer xx-0-Dath-518 (L), MN915930, MN904292, MN915422, MN916176, MN915680; P. fraternus G.L.Webster, Pakistan, Nooteboom 3010 (L), MN915931, –, MN915423, MN916306, MN915681; P. friesii Hutch., Zambia, Harder *et al.* 2778 (WAG), MN915932, MN904293, MN915424, MN916177, MN915682; P. fuernrohrii F. Muell., Australia, Coveny 13478 (NE), –, MN904294, –, MN916178, –; P. fuscoluridus Müll.Arg. var. fuscoluridus (Phyllanthus fuscoluridus 2), Madagascar, Schatz 1737 (WAG), MN915934, MN904296, MN915426, MN916179, –; P. fuscoluridus Müll.Arg. var. villosus (Leandri) Ralim. & Petra Hoffm. (Phyllanthus fuscoluridus 1), Madagascar, Dorr 3650 (WAG), MN915933, MN905068, MN915425, MN916180, –; P. aff. fuscoluridus Müll.Arg., Madagascar, Ravelonarivo 3808 (MO), MN915845, MN904295, MN915329, MN916282, –; P. gabonensis Jean F.Brunel (Phyllanthus gabonensis 1), Gabon, Maas 10095 (WAG), –, MN904299, MN915427, MN916181, MN915683; P. gabonensis Jean F.Brunel (Phyllanthus gabonensis 2), Gabon, Wieringa 8492 (WAG), –, MN915935, MN904313, MN915428, MN916182; P. gardnerianus (Wight) Baill., Sri Lanka, Kathriarachchi *et al.* 42 (K), AY936694, MN904314, MN915429, AY936598, MN915684; P. geoffrayi Beille, Thailand, Larsen *et al.* 3259 (L), MN915936, MN904315, MN915430, MN935816, MN915685; P. gillettianus Jean F.Brunel, Namibia, Germishuizen 9727 (WAG), MN915937, MN904316, MN915431, –, MN915686; P. glaucophyllus Sond. (Phyllanthus glaucophyllus 1), Guinea, Van der Brugt 1156 (WAG), MN915938, MN904317, MN915432, MN916183, MN915687; P. glaucophyllus Sond. (Phyllanthus glaucophyllus 2), Guinea, Haba 123 (WAG), MN915939, MN904318, MN915433, MN916340, MN915688; P. glaucus Wall. ex Müll.Arg. (Phyllanthus glaucus 2), China, Hong Kong, Bouman & Liu RWB028 (L), MN915940, MN904291, MN915434, MN916175, MN915689; P. [subg. Gomphidium] sp. (Phyllanthus cf. Gomphidium sp.), Philippines, Yu 250 (L), MN915889, MN904253, MN915377, MN916148, MN915640; P. gomphocarpus Hook.f., Malaysia, Klackenberg & Lundin 579 (L), MN915941, MN905073, MN915435, MN916184, –; P. grandisepalus F.Muell. ex Müll.Arg., Australia, Albrecht 13268 (NE), MN915942, MN904319, MN915436, MN916289, MN915690; "P. graniticola" msc. name, sp. nov.,Australia, Telford 13004 (NE),MN915943,MN904320,MN915437,MN916185, MN915691; P. graveolensKunth, Ecuador, Klitgaard *et al.* 399 (K), AY936696, MN904321, MN915438, AY936600, MN915692; P. guillauminii Däniker, New Caledonia, Kawakita 273 (KYO), –, FJ235353, –, FJ235261, –; P. gunnii Hook.f., Australia, Coveny 11474 (L), MN915944, MN904322, MN915439, MN916290, MN915693; P. harrisii Radcl.- Sm., Tanzania, Zanzibar, Faulkner 3179 (WAG), MN915945, MN904323, MN915440, MN916341, MN915694; P. hebecarpus Benth., Australia, Copeland NE66669 (NE), –, MN904324, –, MN916308, MN915695; P. heliotropus C.Wright ex Griseb., Cuba, Maas *et al.* 7762 (U), MN915946, MN904325, MN915441, MN916186, MN915696; P. hirtellus F.Muell. ex Müll.Arg., Australia, Pedersen 1328 (L), MN915947, MN904326, MN915442, MN916187, MN915697; P. humbertii (Leandri) Petra hoffm. & McPherson, Madagascar, Kawakita 235 (KYO), –, FJ235345, –, FJ235253, –; P. hutchinsonianus S.Moore (Phyllanthus hutchinsonianus 1), Zimbabwe, Poilecot 7974 (K), AY936697,

MN904327, MN915443, AY936601, MN915698; P. hutchinsonianus S.Moore (Phyllanthus hutchinsonianus 2), Zimbabwe, Bamps 88 (WAG), MN915948, MN904306, MN915444, –, –; P. hypospodius F.Muell., Australia, Bruhl *et al.* 1123 (L), –, GQ503435, GQ503495, EU643744, GQ503559; P. juglandifolius Willd., Netherlands, Hortus botanicus Amsterdam, cultivated, Bouman RWB16 (L), MN915949, MN904328, MN915445, MN916188, MN915699; P. kaessneri Hutch., Tanzania, Pocs 89182 (K), AY936700, –, –, AY936603, –; P. kanalensis Baill., New Caledonia, McPherson & Van der Werff 17886 (K), AY936701, –, –, AY936604, –; P. kaweesakii Pornp., Chantar. & J.Parn., Thailand, Pornpongrungrueng & Triyuttachai 1174 (KKU), KY091120, –, –, KY091108, –; P. kerstingii Jean F.Brunel (Phyllanthus kerstingii 1), Guinea, Darbyshire 562 (WAG), MN915950, MN905074, MN915447,MN916189,MN915701; P. kerstingii Jean F.Brunel (Phyllanthus kerstingii 2), Guinea, Malaisse 14792 (WAG),MN915951, –,MN915448, –,MN915702; P. kidna Challen&PetraHoffm., Cameroon, Cheek 11531 (K), FR715993, –, –, FR715992, –; P. kinabalucius Airy Shaw, Malaysia, Sabah, Van der Ent (Kinabalu Parcs living collection), no voucher, MN915952, MN904330, MN915449, MN916190, MN915703; P. klotzschianus Müll.Arg., Brazil, Grappo *et al.* 780 (K), AY936702, –, –, AY936605, –; P. cf. klotzschianus Müll.Arg., Brazil, Carneiro 10 10 (K), –, –, MN915450, –, MN915641; P. koniamboensis M.Schmid, New Caledonia, Kawakita 277 (KYO), –, FJ235350, –, FJ235258, –; P. koumacensis Guillaumin, New Caledonia, McPherson 19163A (MO), MN915953, MN904331, MN915451, MN916191, –; P. laciniatus C.B.Rob., Philippines, Agoo 5660 (L), MN915954, MN904332, MN915452, MN916192, MN915705; P. lacunarius F.Muell., Australia, Bates 62700 (NE), MN915955, MN904333, MN915453, MN916312, MN915706; P. lacunellus Airy Shaw, Australia, Bates 62500 (NE), MN915956, MN904334, MN915454, MN916313, MN915707; P. lamprophyllus Müll.Arg. (Phyllanthus lamprophyllus 1), Philippines, Agoo 5592 (L), MN915957, MN904335, MN915455, MN916193, MN915708; P. lamprophyllus Müll.Arg. (Phyllanthus lamprophyllus 2), Australia, Telford & Bruhl 13049 (L), MN915958, MN904336, MN915456, MN916194, MN915709; P. lamprophyllus Müll.Arg. (Phyllanthus lamprophyllus 3), Australia, Telford & Bruhl 13051 (L), MN915959, MN904337, MN915457, MN916195, MN915710; P. lamprophyllus Müll.Arg. (Phyllanthus lamprophyllus 4), Singapore, Singapore botanical garden, Yu 161 (L), MN915960, MN904338, MN915458, MN916309, MN915711; P. leptoclados Benth., China, Yunnan, Xishuangbanna Tropical Botanical Garden, Bouman & Yong RWB051 (HITBC), MN915961, MN904339, MN915459, MN916196, MN915712; P. leucanthus Pax (Phyllanthus leucanthus 1), Eritrea, de Wilde 4604 (WAG), MN915962, MN904300, MN915460, MN916149, MN915642; P. leucanthus Pax (Phyllanthus leucanthus 2), Ethiopia, Friis 8619 (WAG), MN915963, MN904340, MN915461, MN916344, MN915713; P. leucocalyx Hutch. (Phyllanthus leucocalyx 1), Tanzania, Bidgood 7161 (WAG), –, MN904341, MN915462, MN916197, –; P. leucocalyx Hutch. (Phyllanthus leucocalyx 2), Tanzania, Bidgood 6969 (WAG),

MN915964, MN904342, MN915463, MN916198, –; P. lichenisilvae (Leandri ex Humbert) Petra Hoffm. & McPherson, Madagascar, Antilahimena 7638 (MO), –, MN904343, MN915464, MN916199, –; P. ligustrifolius S.Moore (Phyllanthus ligustrifolius 1), New Caledonia, McPherson 19091 (MO), MN915965, MN904344, MN915465, MN916310, –; P. ligustrifolius S.Moore (Phyllanthus ligustrifolius 2), New Caledonia, McPherson 5025 (L), MN915966, MN904309, MN915466, MN916311, MN915714; P. limmuensis Cufod., Ethiopia, de Wilde 6524 (WAG), MN915967, MN904345, MN915467, MN916291, MN915715; P. lindenianus Baill., Dominican Republic, Fuertes 345 (K), –, –, MN915468, MN916200, MN915716; P. loandensis Welw. ex Müll.Arg. (Phyllanthus loandensis 1), Malawi, Pawek R597 (WAG), MN915968, MN904346, MN915469, MN916201, MN915717; P. loandensis Welw. ex Müll.Arg. (Phyllanthus loandensis 2), Malawi, Pawek 12535 (WAG), MN915970, MN904297, MN915470, MN916202, MN915718; P. loandensis Welw. ex Müll.Arg. (Phyllanthus loandensis 3), Mozambique, Nuvunga 526 (WAG), MN915969, MN905072, MN915471, MN916203, MN915719; P. lokohensis Leandri, Madagascar, Antilahimena 8041 (MO), MN915971, MN904347, –, MN916316, –; P. loranthoides Baill., New Caledonia, MacKee 31810 (K), AY936705, –, –, AY936607, –; *P. macranthus* Pax, Zimbabwe, *Biegel et al. 4847* (WAG), MN915972, MN905075, MN915472, MN916292, MN915720; *P. madagascariensis* Müll.Arg., Madagascar, McPherson 18925 (MO), MN915973, MN904348, MN915473, MN916317, –; P. madeirensis Croizat, Brazil, Vincentini 1206 (U), MN915974, MN905078, MN915474, MN916293, MN915721; *P. maderaspatensis* L., Madagascar, *Hunter et al. 1532* (K), AY936707, –, –, AY936609, –; *P. magnificens* Jean F.Brunel & J.P.Roux, Guinea, *van der Burgt 1196* (WAG), MN915975, MN904349, MN915475, MN916345, MN915722; *P. magudensis* Jean F.Brunel, Sudan, *Blokhuis 50* (WAG), MN915976, MN904350, MN915476, MN916318, MN915723; *P. mangenotii* M.Schmid, New Caledonia, *Kawakita 270* (KYO), –, FJ235349, –, FJ235257, –; *P. mannianus* Müll.Arg. (*Phyllanthus mannianus* 1), Cameroon, *Raynal 12256* (WAG), MN915977, MN904351, MN915477, MN916347, MN915724; P. mannianus Müll. Arg. (*Phyllanthus mannianus* 2), Cameroon, *Biye 129* (WAG),MN915978,MN904352,MN915478, –,MN915726; *P. mantadiensis* Ralim. &PetraHoffm. (*Phyllanthus mantadiensis* 1),Madagascar, *Rasoazanany 110* (MO),MN915979,MN904353,MN915479,MN916204, –; *P. mantadiensis* Ralim. & Petra Hoffm. (Phyllanthus mantadiensis 2), Madagascar, *Rasoazanany 514* (MO), MN915980, MN904354, MN915480, MN916319, –; P. marojejiensis (Leandri) Petra Hoffm. & McPherson, Madagascar, Kawakita 243 (KYO), –, FJ235346, –, FJ235254, –; *P. matitanensis* Leandri, Madagascar, *Ravelonarivo 4276* (MO), MN915981, MN904355, MN915481, MN91602.

Supplementary figure 7-S1. A. Bayesian majority-rule consensus tree with branches transformed of the nuclear (ITS, PHYC) dataset for *Phyllanthus* and related genera, posterior probabilities (PP) are displayed at the nodes, clade labels follow Fig. 7-4; B. Bayesian majority-rule consensus displaying branch length. — New undescribed species are indicated with an asterisk.
tax12424-sup-0006-FigureS1.pdf

Supplementary figure 7-S2. A. Bayesian majority rule consensus tree with branches transformed of the chloroplast (*accD–psaI*, *matK* and *trnS–trnG*) dataset for *Phyllanthus* and related genera with branches transformed, posterior probabilities (PP) are displayed at the nodes, clade labels follow Figure 7-4; B. Bayesian majority rule consensus displaying tree branch. — New undescribed species are indicated with an asterisk.
tax12424-sup-0007-FigureS2.pdf

Supplementary figure 7-S3. A. Bayesian majority rule consensus tree with branches transformed of the nuclear (ITS) dataset for *Phyllanthus* and related genera with branches transformed, posterior probabilities (PP) are displayed at the nodes, clade labels follow Figure 7-4, relationship between subgenus *Betsileani* and part of subgenus *Gomphidium* is highlighted in colour; B. Bayesian majority rule consensus displaying branch length. — New undescribed species are indicated with an asterisk.
tax12424-sup-0008-FigureS3.pdf

Supplementary figure 7-S4. A. Bayesian majority rule consensus tree with branches transformed of the nuclear (*PHYC*) dataset for *Phyllanthus* and related genera with branches transformed, posterior probabilities (PP) are displayed at the nodes, clade labels follow Figure 7-4; B. Bayesian majority rule consensus displaying branch length. — New undescribed species are indicated with an asterisk.
tax12424-sup-0009-FigureS4.pdf

Supplementary figure 7-S5. A. Bayesian majority rule consensus tree with branches transformed of the chloroplast (*accD-psaI*) dataset for *Phyllanthus* and related genera with branches transformed, posterior probabilities (PP) are displayed at the nodes, clade labels follow Figure 7-4; B. Bayesian majority rule consensus displaying branch length. — New undescribed species are indicated with an asterisk.
tax12424-sup-0010-FigureS5.pdf

Supplementary figure 7-S6. A. Bayesian majority rule consensus tree with

branches transformed of the chloroplast (*matK*) dataset for *Phyllanthus* and related genera with branches transformed, posterior probabilities (PP) are displayed at the nodes, clade labels follow Figure 7-4; B. Bayesian majority rule consensus displaying branch length. — New undescribed species are indicated with an asterisk.
tax12424-sup-0011-FigureS6.pdf

Supplementary figure 7-S7. A. Bayesian majority rule consensus tree with branches transformed of the chloroplast (*trnS-trnG*) dataset for *Phyllanthus* and related genera with branches transformed, posterior probabilities (PP) are displayed at the nodes, clade labels follow Figure 7-4; B. Bayesian majority rule consensus displaying branch length. — New undescribed species are indicated with an asterisk.
tax12424-sup-0012-FigureS7.pdf

Supplementary figure 7-S8. Bayesian majority rule consensus tree with branches transformed of the combined nuclear (ITS and *PHYC*) and chloroplast (*accD–psaI*, *matK* and *trnS–trnG*) datasets for *Phyllanthus* with related genera reduced to only include samples with 3 out of 5 markers, posterior probabilities (PP) are displayed at the nodes, infrageneric classification follows Bouman *et al.* (2018a); subgenera are given above colored clades, sections to the right. — New undescribed species are indicated with an asterisk.
tax12424-sup-0013-FigureS8.pdf

Supplementary figure 7-S9. Maximum Likelihood bipartitions tree with branches transformed of the combined nuclear (ITS and *PHYC*) and chloroplast (*accD–psaI*, *matK* and *trnS–trnG*) datasets for *Phyllanthus* and related genera with branches transformed, ML scores are displayed at the nodes, clade labels follow Figure 7-4. — New undescribed species are indicated with an asterisk.
tax12424-sup-0014-FigureS9.pdf

Supplementary figure 7-S10. Basis for Figure 7-4, bayesian majority rule consensus tree of the full combined nuclear (ITS and *PHYC*) and chloroplast (*accD–psaI*, *matK* and *trnS–trnG*) datasets for *Phyllanthus* and related genera, posterior probabilities (PP) are displayed at the nodes, infrageneric classification follows Bouman *et al.* (2018a); subgenera are given above colored clades, sections to the right.
tax12424-sup-0015-FigureS10.pdf

Supplementary appendix S1. DNA matrix of ITS marker of *Phyllanthus* and related genera.

tax12424-sup-0001-AppendixS1.nex

Supplementary appendix S2. DNA matrix of *PHYC* marker of *Phyllanthus* and related genera.
tax12424-sup-0002-AppendixS2.nex

Supplementary appendix S3. DNA matrix of *accD-psaI* marker of *Phyllanthus* and related genera.
tax12424-sup-0003-AppendixS3.nex

Supplementary appendix S4. DNA matrix of *matK* marker of *Phyllanthus* and related genera.
tax12424-sup-0004-AppendixS4.nex

Supplementary appendix S5. DNA matrix of *trnS-trnG* marker of *Phyllanthus* and related genera. A section of ambiguous alignment was excluded from our analyses, but is still included here in the matrix at positions 259–413. Matrix used for analysis used the positions as specified in the charactersets.
tax12424-sup-0005-AppendixS5.nex