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A revised phylogenetic classification of tribe Phyllantheae (Phyllanthaceae)

RODERICK W. BOUMAN[1,2,3,10*], PAUL J.A. KEBLER[2,3,11], IAN R.H. TELFORD[4,12], JEREMY J. BRUHL[4,13], JOERI S. STRIJK[5,6,14], RICHARD M.K. SAUNDERS[7,15], HANS-JOACHIM ESSER[8,16], BANESSA FALCÓN-HIDALGO[9,17] & PETER C. VAN WELZEN[1,3,18]

[1]*Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands*
[2]*Hortus botanicus Leiden, Leiden University, PO Box 9500, 2300 RA Leiden, The Netherlands*
[3]*Institute of Biology Leiden, Leiden University, PO Box 9505, 2300 RA Leiden, The Netherlands*
[4]*Botany and N. C. W. Beadle Herbarium, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia*
[5]*Institute for Biodiversity and Environmental Research, Jalan Tungku Link, Universiti Brunei Darussalam, Brunei Darussalam*
[6]*Alliance for Conservation Tree Genomics, Pha Tad Ke Botanical Garden, PO Box 959, 06000 Luang Prabang, Lao PDR*
[7] *Division of Ecology & Biodiversity, School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong, China*
[8]*Botanische Staatssammlung München, Menzinger Strasse 67, D-80638 München (Munich), Germany*
[9]*Jardin Botánico Nacional, Unisversidad de La Habana, Carretera "El Rocío" km 3.5, Calabazar, Boyeros, La Habana, Cuba*
[10] *r.w.bouman@hortus.leidenuniv.nl*; *https://orcid.org/0000-0002-2949-3318*
[11] *p.j.a.kessler@hortus.leidenuniv.nl*; *https://orcid.org/0000-0001-6569-4726*
[12] *itelford@une.edu.au*; *https://orcid.org/0000-0002-3570-0053*
[13] *jbruhl@une.edu.au*; *https://orcid.org/0000-0001-9112-4436*
[14] *jsstrijk@actg.science*; *https://orcid.org/0000-0003-1109-7015*
[15] *saunders@hku.hk*; *https://orcid.org/0000-0002-8104-7761*
[16] *esser@snsb.de*; *https://orcid.org/0000-0001-6518-8612*
[17] *banessa@fbio.uh.cu*; *https://orcid.org/0000-0003-2519-3278*
[18] *peter.vanwelzen@naturalis.nl*; *https://orcid.org/0000-0002-5072-431X*
**Corresponding author*

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RODERICK W. BOUMAN, PAUL J.A. KEBLER, IAN R.H. TELFORD, JEREMY J. BRUHL, JOERI S. STRIJK, RICHARD M.K. SAUNDERS, HANS-JOACHIM ESSER, BANESSA FALCÓN-HIDALGO & PETER C. VAN WELZEN

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Abstract

The majority of tribe Phyllantheae (Phyllanthaceae) is currently placed in the paraphyletic genus *Phyllanthus* and discussions have persisted on how to resolve this issue. Here, we split *Phyllanthus* into ten monophyletic genera, which are all reinstatements of former genera, but with changes made to the circumscription and constituent species of each group. The genera *Breynia*, *Glochidion* and *Synostemon* were recently found to be nested within *Phyllanthus* and discussions ensued whether or not to subsume everything into *Phyllanthus* s.l. Instead of combining all these genera, we here implement the solution of splitting *Phyllanthus* into strictly monophyletic genera to ensure that the classification is consistent with the latest phylogenetic results. The new classification is based on a phylogenetic framework combined with differences in habit, branching type, floral, fruit and pollen morphology. With this new division of the genus *Phyllanthus*, tribe Phyllantheae will consist of the following 18 genera: *Breynia*, *Cathetus*, *Cicca*, *Dendrophyllanthus*, *Emblica*, *Flueggea*, *Glochidion*, *Heterosavia*, *Kirganelia*, *Lingelsheimia*, *Lysiandra*, *Margaritaria*, *Moeroris*, *Nellica*, *Nymphanthus*, *Phyllanthus*, *Plagiocladus* and *Synostemon*. As a result of the reinstated genera, five new names for illegitimate combinations or previous overlooked nomenclatural anomalies and 645 new combinations are proposed. Several keys are provided to distinguish the reinstated genera. Full species lists are given for the reinstated genera treated here except for *Breynia*, *Synostemon* and *Glochidion*.

Introduction

The classification of the family Phyllanthaceae by Hoffmann *et al.* (2006) was a comprehensive work that brought together results from morphological and phylogenetic studies. However, discussions have persisted regarding the largest tribe of the family, as its largest genus, *Phyllanthus* Linnaeus (1753: 981), is paraphyletic (Kathriarachchi *et al.* 2006). The genera *Breynia* Forster & Forster (1776: 145) (including species formerly assigned to *Sauropus* Blume 1826: 595), *Glochidion* Forster & Forster (1776: t.57) and *Synostemon* Mueller (1859: 32) are nested within *Phyllanthus* (Kathriarachchi *et al.* 2006), which has sparked discussion on how to resolve this. Although Kathriarachchi *et al.* (2006) and Hoffmann *et al.* (2006) proposed combining *Phyllanthus* with the genera nested within it, this would lead to a morphologically heterogeneous genus with more than 1200 species (van Welzen *et al.* 2014). Some name changes for this decision have already been implemented for local floras (e.g., Chakrabarty & Balakrishnan 2009, Wagner & Lorence 2011, Kurosawa 2016). However, some argue that this would make *Phyllanthus* s.l. too variable and an unwieldy genus (e.g., Pruesapan *et al.* 2008, 2012). An alternative approach to resolving paraphyly is to retain the nested genera as distinct taxa and to split *Phyllanthus* into new, monophyletic and morphologically recognizable genera (Pruesapan *et al.* 2008, 2012, van Welzen *et al.* 2014, Bouman *et al.* 2021). Pruesapan *et al.* (2012), in a more extensive phylogeny of *Breynia* (including *Sauropus*) and *Synostemon*, resolved these genera as monophyletic and suggested they be retained as genera, which incurred further name changes (Chakrabarty & Balakrishnan 2012, van Welzen *et al.* 2014). Unfortunately, this still leaves the remainder of the genus *Phyllanthus* as a paraphyletic group, badly in need of resolution.

The genus *Phyllanthus* as currently circumscribed contains almost 900 species (Bouman *et al.* 2018b), and displays an enormous diversity both in vegetative and floral characters (Webster 1956). Some species were originally placed in separate genera due to their morphological distinctiveness (see Baillon 1858), but were combined in a broad definition of *Phyllanthus* by Müller (1863, 1866). The extensive morphological diversity within *Phyllanthus* was reflected in numerous sections (Müller 1866), which were usually former genera. These sections were subsequently grouped into subgenera (Webster 1956, 1957, 1958), but new insights from palynological (Punt 1967, 1972, 1980, 1986, 1987, Meewis & Punt 1983, Lobreau-Callen *et al.* 1988, Webster & Carpenter 2002, 2008) and phylogenetic research (Kathriarachchi *et al.* 2006, Pruesapan *et al.* 2008, 2012, Falcón *et al.* 2020, Bouman *et al.* 2021) resulted in many changes to this classification. A large number of species transfers were not implemented and there were no lists of the species in each group. Bouman *et al.* (2018) compiled a list that shows the placements of almost all *Phyllanthus* species based on previous morphological, phylogenetic and taxonomic work. The paper aimed to correct some common misconceptions and provide a workable system for the rest of *Phyllanthus*. Still some remaining issues were discussed in the paper and these require taxonomic and nomenclatural changes (e.g., previously paraphyletic sections and possibly polyphyletic subgenera). Nevertheless, the various subgenera and sections are based on genera formerly recognized as separate from *Phyllanthus* (e.g., *Cicca* in Ridley 1924) and these names provide ideal candidates when deciding on

new generic boundaries. According to the synopsis of Bouman *et al.* (2018), *Phyllanthus* consisted of 18 subgenera and 70 sections. Several subgenera are similar as they are sister clades (e.g., subgenus *Swartziani* (G.L.Webster 1955: 53) Ralimanana & Hoffmann (2013: 536) and subgenus *Afroswartziani* Ralimanana & Hoffmann 2013: 538), while others are superficially similar due to convergent evolution (e.g., subgenus *Macraea* (Wight 1852: 27) Brunel (1987: 293) and subgenus *Phyllanthus* section *Loxopodium* Webster 1955: 46). Related and morphologically similar subgenera do not warrant separate recognition. This approach will result in fewer new genera than the estimated 20 clades in Kathriarachchi *et al.* (2006).

Here we aim to resolve the paraphyly of *Phyllanthus* and address all known subgeneric problems in the genus. As we consider that subsuming *Breynia*, *Synostemon* and *Glochidion* in *Phyllanthus* is unwarranted and maintaining a paraphyletic genus is also not a desirable solution, we implement an alternative solution, a new classification of 18 genera in tribe Phyllantheae: *Breynia*, *Cathetus* Loureiro (1790: 608), *Cicca* Linnaeus (1767: 124), *Dendrophyllanthus* Moore (1921: 395), *Emblica* Gaertner (1790: 122), *Flueggea* Richard (1807: 8), *Glochidion*, *Heterosavia* (Urbach 1902: 284) Hoffmann (2008: 152), *Kirganelia* de Jussieu (1789: 387), *Lingelsheimia* Pax (1909b: 317), *Lysiandra* (Mueller 1859: 108) R.W.Bouman, I.Telford & J.J.Bruhl, *Margaritaria* L.f. (1782: 428), *Moeroris* Rafinesque (1838: 91), *Nellica* Rafinesque (1838: 92), *Nymphanthus* Loureiro (1790: 543), *Phyllanthus*, *Plagiocladus* Brunel (1987: 260) and *Synostemon* (Table 1). Many new nomenclatural combinations are necessary to implement this taxonomic change, which are here included for each group together with all currently accepted species (except for *Glochidion*, *Breynia* and *Synostemon*).

TABLE 1. List of genera in tribe Phyllantheae with global distribution and (estimated) number of species for each group.

Genus	Distribution	Number of species
Breynia J.R.Forst. & G.Forst.	Australia, mainland Asia, Malesia	89
Cathetus Lour.	Africa, mainland Asia, Malesia, Australia and Pacific	40
Cicca L.	Africa, Asia, Madagascar, South America (1 widely cultivated species)	45
Dendrophyllanthus S.Moore	Australia, (Eastern) Malesia, Pacific	161
Emblica L.	Australia, mainland Asia, Malesia (1 invasive and 1 widely cultivated species)	45
Flueggea Willd.	Pantropical	16
Glochidion J.R.Forst. & G.Forst.	Australia, mainland Asia, Malesia, Pacific	~350
Heterosavia (Urb.) Petra Hoffm.	West Indies	4
Kirganelia A.Juss.	Africa, Madagascar, mainland Asia, Malesia and Australia	24
Lingelsheimia Pax	Madagascar, Tropical Africa	6
Lysiandra (F.Muell.) R.W.Bouman, I.Telford & J.J.Bruhl	Australia	25
Margaritaria L.f.	Pantropical	13
Moeroris Raf.	South, Central, North America, Tropical Africa, Madagascar (few widely invasive species)	199
Nellica Raf.	Africa, Central and North America	20
Nymphanthus Lour.	Australia, mainland Asia, Malesia	86
Phyllanthus L.	Americas, West Indies (some tropical invasives)	213
Plagiocladus Jean F.Brunel	Tropical Africa (Gabon)	1
Synostemon F.Muell.	Australia, mainland Asia, Malesia	41

Methods and results

The following new classification is based on Falcón *et al.* (2020) and Bouman *et al.* (2021) and a new phylogenetic analysis using the data from both studies. This combinend dataset comprises two nuclear DNA regions (the Internal Transcribed Spacers region referred to as ITS, including 5.8S, and the low copy *PHYC*) and three plastid regions (*accD-psaI*, *trnS-trnG* intergenic spacers, and *matK* with portions of the flanking *trnK* intron). GenBank accession

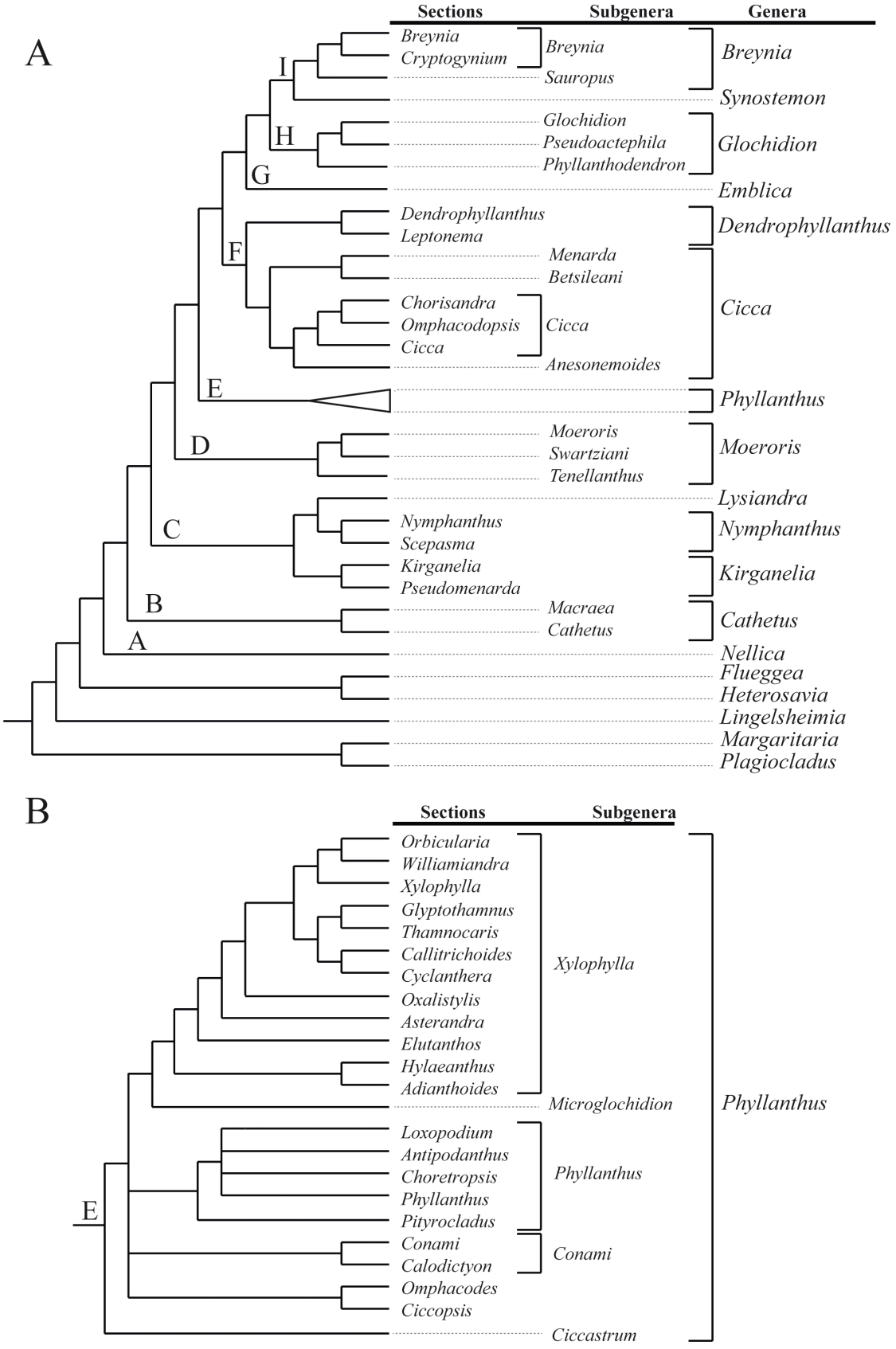


FIGURE 1. (**A**) Summary phylogeny showing relations between genera in tribe Phyllantheae from Bayesian and Maximum Likelihood analysis of five markers (ITS, *PHYC, accD–psaI*, *trnS–trnG, matK*), modified from Appendix 1. Classification is shown of genera (right column), subgenera (middle column) and sections (except for the genus *Phyllanthus*. Sections not included in phylogenetic analyses and those for the genus *Flueggea* were omitted. (**B**) summary phylogeny of the genus *Phyllanthus* as envisioned here with subgenera and sections of groups included in phylogenetic studies shown.

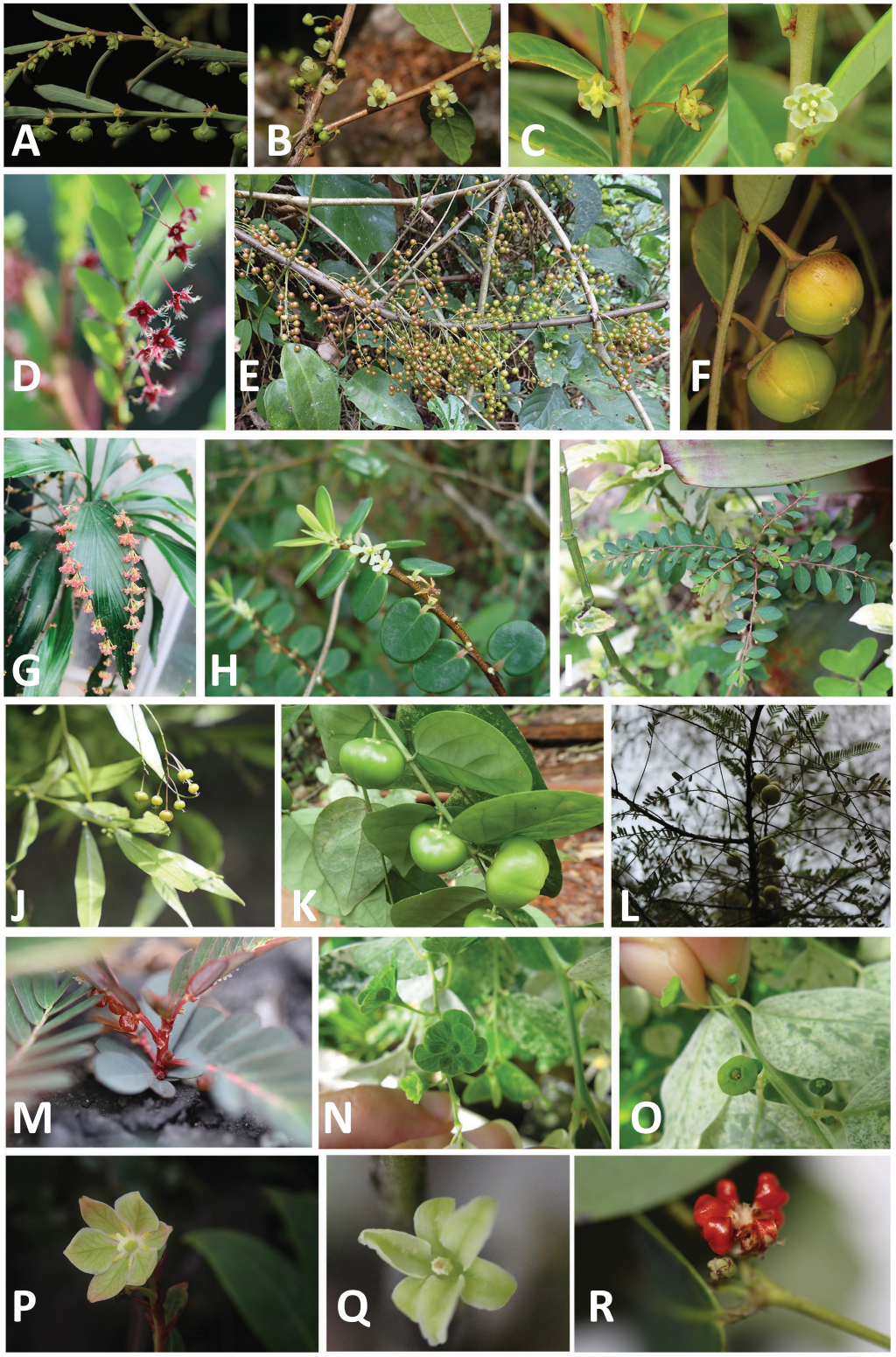


FIGURE 2. Images of representative members of tribe Phyllantheae. (A) Flowers of *Nellica maderaspatensis*. (B) Pistillate flowers of *Cathetus gracilis*, note the unique disc covering the ovary. (C) Pistillate and staminate flowers of *Cathetus glaucophyllus*. (D) Staminate flowers of *Nymphanthus glaucescens*. (E) Fruits of *Kirganelia muelleriana*. (F) Fruits of *Lysiandra subcrenulata*. (G) Phylloclade with flowers of *Phyllanthus angustifolius*. (H) Flowering branchlet of *Phyllanthus incrustatus*, note the ornamentation on the axes. (I) Habit of *Moeroris tenella*. (J) Fruiting branch of *Dendrophyllanthus tenuirhachis*. (K) Fruits of *Cicca profusa*. (L) Fruiting branch of *Emblica officinalis*. (M) Flowering plant of *Emblica urinaria*. (N) Pistillate flower of *Breynia disticha*. (O) Staminate flower of *Breynia disticha*. (P) flower of *Glochidion dunnianum*. (Q) Staminate of *Glochidion lanceolarium*. (R) Dehisced capsule of *Glochidion* sp. showing seeds covered with a red sarcotesta. Photos: A & F by J.J. Bruhl; B & P by M.S. Nuraliev; C by T. Williams; E & K by C. Jongkind; H by B. Falcón; J by R.-Y. Yu; D, G, I, L, M, N, O, Q & R by R.W.Bouman.

numbers are given in Appendix 2. Alignment length of ITS and *matK* did not change from Bouman *et al.* (2021) after incorporating relevant sequences from Falcón *et al.* (2020). Sequences were downloaded from Genbank and added to the matrices available from Bouman *et al.* (2021, Appendices S1-S5) using Mesquite V. 3.61 (Maddison & Maddison 2019). The new sequences were aligned to the existing matrices using the Pairwise Aligner tool and then manually corrected for alignment errors in PAUP v4.0a (Swofford 2002). The combined dataset containing 416 terminals was analysed with 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 following methods described in Bouman *et al.* (2021). A summary tree showing the generic relationships between groups is presented in Fig. 1. Compared to Bouman *et al.* (2018b), a few species are treated here in different groups as a result of new phylogenetic and morphological information. These are not discussed in the text, but are briefly highlighted in Appendix 1. The latest phylogeny of *Phyllanthus* and its related genera (the basis for Figure 1) is presented in Supplementary Figure 1 with the voucher data summarized in Appendix 2. The addition of new sequences from Falcón *et al.* (2020) had some effect on node support, but did not affect relationships between major groups and the phylogeny was comparable to Bouman *et al.* (2021). Descriptions of groups are compiled from personal observations in combination with past taxonomic treatments (e.g., Webster 1956, 1957, 1958, 2001a, b, 2002a, b, 2003, 2004, Airy Shaw 1975, 1980, Brunel & Roux 1977, 1981, McPherson & Schmid 1991, Radcliffe-Smith 2001, Santiago *et al.* 2006, Ralimanana & Hoffmann 2011, 2014, Ralimanana *et al.* 2013, Verwijs *et al.* 2019, Ralimanana & Cable 2020). Pollen data is gathered from several studies (e.g., Meewis & Punt 1983, Brunel 1987, Lobreau-Callen *et al.* 1988, Webster & Carpenter 2002, 2008, Sagun & van der Ham 2003, Wu *et al.* 2016). A key for all genera in subtribe Phyllanthaeae is provided as well as keys for the three major distribution areas, Americas, Africa to Middle East and Asia to Pacific.

Taxonomic treatment

The following is the implementation of a new classification for *Phyllanthus* s.l. including *Breynia*, *Glochidion* and *Synostemon*. The application of the Shenzhen Code (Turland *et al.* 2018) results in name changes to several autonymic sections following article 22.1, such as *Kirganelia* section *Anisonema*, which becomes *Kirganelia* section *Kirganelia*. Some reinstated genera have different names than their subgeneric names as part of *Phyllanthus* due to the priority of the oldest name per classification level (e.g., the genera *Cathetus*, *Dendrophyllanthus*, *Moeroris* and *Nymphanthus*). Other genera, not part of the former *Phyllanthus* complex, were already previously separated and treated by other authors (e.g., *Flueggea*, Webster 1984, *Heterosavia*, Hoffmann 2008, *Margaritaria*, Webster 1979, *Plagiocladus*, Brunel 1987, Hoffmann *et al.* 2006). The genera *Breynia*, *Synostemon* and *Glochidion* are also mentioned briefly, but a more complete treatment of the nomenclature for the genera *Breynia* and *Synostemon* can be found in van Welzen *et al.* (2014). Species transfers follow the format of the new combination name followed by the basionym and, if different, the synonym under *Phyllanthus* that was previously used. For each taxonomic group, all currently accepted species are included and also listed with the taxonomic changes, species numbers per genus are given in brackets after the header "Included species and taxonomic changes" and shown in Table 1. Where appropriate, notes are given to explain the placement or transfer of species and the affinities between various groups. Examples of representative members of the various genera are shown in Figure 2.

1. Key to the genera of tribe Phyllantheae

With the following key the genera of tribe Phyllantheae can be identified, but it does not take into account any exceptions or subgenera and (sub)sections. An asterisk (*) denotes parts of the key that are not dichotomous.

1. Pistillode present in staminate flowers 2
1. Pistillode absent in staminate flowers 5

2. Stamens > 10—Africa & Madagascar ..... *Lingelsheimia*
2. Stamens 4–7 3

3. Branching non-phyllanthoid (laminate leaves and flowers on all axes, branchlets not deciduous); staminate sepals 4–7 (usually 5), stamens 4–7, filaments free or fused for half of length; anther connectives non-apiculate; fruits capsules or baccate 4
3. Branching phyllanthoid (leaves on main stem reduced to scales, = cataphylls, laminate leaves and flowers on lateral axes, lateral branchlets deciduous); staminate sepals 4, stamens 4, filaments connate, anther connectives apiculate; fruits capsules—Asia ..... *Glochidion* (*G. moi*)

4. Petals absent; fruits with 2 seeds per locule; pollen exine verruculose—Pantropical ..... *Flueggea*
4. Petals present; fruits with 1 or 2 seeds per locule; pollen exine reticulate—West Indies ..... *Heterosavia*

5. Disc absent (sepal scales may be present, these close flower when anthers are unripe, no glandular function) 6
5. Disc / disc glands present 10

6. Inflorescences on specialized leafless axes; staminate sepals 4, stamens (2–)3–4(–5), filaments free; fruits indehiscent, woody or drupaceous ..... subgenus *Cicca* section *Cicca*
6. Inflorescences in axils of leaves to cauliflorous; staminate sepals usually 5 or 6, stamens 2–15, filaments free or connate; fruits capsules 7

7. Staminate flowers without sepal scales; filaments free or connate, anther connectives sometimes apiculate; stigmas usually entire or erect and tightly together; ovary 3–15-locular 8
7. Staminate flowers often with sepal scales; filaments connate, anther connectives not apiculate; stigmas usually bifid; ovary 3-locular 9

8. Staminate sepals spreading or united in a tubular shape; disc lobes present; filaments free; ovary 3–5-locular—Malesia ..... *Dendrophyllanthus*
8. Staminate sepals often recurved; disc absent; filaments tightly together (separating as flowers age); ovary 3–15-locular—Australia, mainland Asia, Malesia, Pacific ..... *Glochidion*

9. Sepal scales often present in staminate flowers; fruits wider than long; seeds smooth ..... *Breynia*
9. Sepal scales absent in staminate flowers (except in *Synostemon bacciformis*); fruits longer than wide; seeds sculptured ..... *Synostemon*

10. Branching non-phyllanthoid or sub-phyllanthoid (leaves at base of branchlets not reduced to scales (often in juveniles), lateral branchlets deciduous) 11
10. Branching phyllanthoid 19

11. Stamens > 10—Africa & Madagascar ..... *Lingelsheimia*
11. Stamens 2–5 12

12. Sepals 4; staminate disc entire; stamens 4, filaments free; seeds with blue sarcotesta—Pantropical ..... *Margaritaria*
12. Sepals 5 or 6 (rarely 4, but then with 2 stamens); staminate disc entire or segmented; stamens 2 or 3, filaments free or connate; seeds with no or whitish sarcotesta 13

13. Staminate disc entire (H-shaped in *Moeroris arenaria*) 14
13. Staminate disc segmented into glands 15

14*. Sepals 6 in both sexes; staminate disc urceolate; stamens 3, filaments connate—Asia ..... *Cathetus*
14*. Sepals 6 in both sexes; staminate disc not urceolate; stamens 2, filaments free—Africa ..... *Plagiocladus*
14*. Sepals 4 in staminate flowers, 6 in pistillate flowers; staminate disc H-shaped around filaments; stamens 2, filaments free—North America ..... *Moeroris* (*M. arenaria*)

15. Sepals 5; stamens 5, filaments free—Africa ..... *Kirganelia* subgenus *Kirganelia* section *Pseudomenarda*
15. Sepals 5 or 6; stamens usually 3 (rarely 2), filaments connate (free in *Moeroris rosmarinifolius*)—Africa to Asia 16

16. Plagiotropic branchlets caducous, usually fascicled (non-phyllanthoid in section *Elutanthos*, but then with paniculate inflorescences); fruits capsules or berries ..... *Phyllanthus*
16. Plagiotropic branchlets persistent; inflorescences axillary fascicles, never paniculate; fruits capsules 17

17. Leaves on all axes spirally arranged; filaments connate; pistillate disc consisting of free glands—(North America, Africa and Asia/Australia) ..... *Nellica*
17. Leaves on all axes distichous (except at basal nodes in *Cicca*); filaments free or connate; pistillate disc mostly entire (when segmented then filaments mostly free and leaves always distichous) 18

18*. Leaves distichous; pollen 4-colporate; seeds smooth or verrucate—Americas ..... *Phyllanthus* subgenus *Phyllanthus* section *Loxopodium*
18*. Leaves distichous; pollen clypeate; seeds smooth or verrucate—Africa, Asia, Australia and Pacific ... *Cathetus* subgenus *Macraea*
18*. Leaves spiral at basal nodes, distichous at upper nodes; pollen grains perisyncolporate with median pores, colpi bordered by parallel muri; seeds smooth or striate—Madagascar ..... *Cicca* subgenus *Betsileani*

19. Herbs or subshrubs (small plants with woody base) 20
19. Shrubs to trees, rarely climbers 25

20. Inflorescences unisexual 21
20. Inflorescences bisexual 24

21. Pistillate inflorescences on proximal position and staminate inflorescences on distal position on plagiotropic branchlets; seeds transversely ribbed—ovary often covered with tubercles—pantropical, but origin Asia ..... *Emblica* section *Urinaria*
21. Pistillate inflorescences on distal position and staminate inflorescences on proximal position on plagiotropic branchlets; seeds smooth or longitudinally or transversely striate, but not ribbed 22

22. Cataphyllary stipules not auriculate ..... *Phyllanthus*
22. Cataphyllary stipules (unilaterally) auriculate 23

23. Filaments connate, anthers free; seeds smooth or longitudinally striate—Africa ..... *Moeroris*
23. Filaments usually free, sometimes connate, anthers free or connate in a synandrium; seeds smooth, striate or verrucate—South America ..... *Phyllanthus*

24*. Stamens 3, filaments free, anthers dehiscing vertically; pistillate disc entire; pollen 3-syncolporate, exine reticulate; stigmas entire or emarginate; seeds smooth or with faintly striate—Australia, Malesia, Pacific ..... *Dendrophyllanthus* section *Leptonema*
24*. Stamens 2 or 3, filaments entirely or partially connate (free in *M. arenaria*), anthers dehiscing oblique to horizontally (vertically in *M. arenaria*); pistillate disc entire; pollen 3-colporate, exine reticulate; seeds smooth or longitudinally striate—North America, pantropical invasive ..... *Moeroris* subgenus *Swartziani*
24*. Stamens 3, filaments free, anthers dehiscing horizontally; pistillate disc segmented; pollen grains brevicolporate and diorate or porate, exine pilate; seeds verruculose—South America ..... *Phyllanthus* subgenus *Conami* section *Apolepsis*

25. Sepals 4 in staminate flowers; stamens 2, filaments connate, anthers dehiscing horizontally (*Nymphanthus* or *Phyllanthus chryseus*) or vertically (*Phyllanthus* section *Thamnocaris*)—pollen pantoporate or clypeate 26
25. Sepals 5 or 6 in staminate flowers (4 in *Cicca acida*, but then stamens 4, filaments free); stamens 3–15, filaments free or connate, anthers dehiscing mostly vertically, sometimes horizontally 27

26. Inflorescences mostly unisexual; staminate disc segmented; anthers dehiscing horizontally (except in *N. ruber* & *N. touranensis*); pollen pantoporate—Asia ..... *Nymphanthus*
26. Inflorescences unisexual (*P. chryseus*) or bisexual; staminate disc entire (*P. chryseus*) or segmented; anthers dehiscing horizontally (*P. chryseus*) or vertically (*P.* section *Thamnocaris*); pollen clypeate—South America ..... *Phyllanthus*

27. Filaments fused in sets, rarely free (*K. glauca* & *K. flexuosa*), stamens 2 (*K. flexuosa*) or 5, connectives not apiculate; fruits baccate—Africa to Australia ..... *Kirganelia*
27. Filaments never in sets, free or connate, stamens 3–20, connectives sometimes apiculate; fruits capsules or baccate (then with 3 connate stamens) 28

28. Plagiotropic branchlets sometimes differentiated in vegetative (with larger leaves) and floriferous (with smaller leaves) branchlets, pinnatiform; stamens 3, filaments connate, anthers dehiscing vertically, connectives apiculate; pistillate disc segmented—Asia & Pacific ..... *Glochidion*
28. Plagiotropic branchlets not differentiated and all with leaves of similar size (or unifoliate), sometimes bipinnatiform; stamens 3–20, filaments connate or free, anthers dehiscing horizontally to vertically, connectives apiculate or not; pistillate disc entire ..29

29. Branchlets (bi-)pinnatiform; sepals often biseriate (inner whorl much longer); staminate disc often of 3 massive emarginate (or 5 separate) segments to absent, stamens may be inserted on a wide receptaculum; stamens usually 3 or 5 (up to 20 in Pacific species); stigmas mostly entire, rarely bifid—pollen 3–(syn-)colporate 30
29. Branchlets pinnatiform; sepal whorls indistinct; staminate disc segmented or entire; stamens 2–7(–15 in species of South America and West Indies) stigmas usually bifid or lacerate 31

30. Inflorescences fascicles or panicles; sepals 5 or 6, filaments free or connate, anthers dehiscing vertically to obliquely, connectives usually apiculate; pollen 3- or 4-syncolporate, exine rugulose-reticulate, vermiculate, pilate or ± vermiculate—Calyx in fruit sometimes saccate—Malesia, Australia, Pacific ..... *Dendrophyllanthus*
30. Inflorescences fascicles; sepals 6 (5 in *P. tuerckheimii*), filaments connate (free in *P. tuerckheimii*), anthers dehiscing horizontally (vertically in in *P. tuerckheimii*), connectives rarely elongated; pollen diverse, often 3-colporate or porate with diorate colpi (see Webster & Carpenter 2002), exine vermiculate to pilate—Fruits conspicuously veined—South and Central America ..... *Phyllanthus* subgenus *Conami* section *Conami*

31*. Branchlets never transformed to phylloclades; sepals 6; staminate disc segmented; stamens 3, filaments connate, anthers dehiscing vertically, connectives often apiculate; fruits capsules (drupe in *E. officinalis*)—Asia ..... *Emblica*
31*. Branchlets never transformed to phylloclades; sepals 5 or 6; staminate disc segmented; stamens 3, filaments connate, anthers dehiscing mostly horizontally to obliquely, connectives rarely apiculate; fruits capsules—mainly Africa ..... *Moeroris*
31*. Branchlets sometimes transformed to phylloclades; sepals 4–8; staminate disc mostly segmented, sometimes entire; stamens 3–15, filaments free or fused, sometimes fused in several whorls, anthers dehiscing horizontally to vertically, connectives sometimes apiculate; fruits capsules or berries—Americas ..... *Phyllanthus*

2. Keys to the genera based on geographical distribution

The keys below are designed to identify the regional Phyllantheae floras. Some areas have been treated together (i.e., the Americas and the West Indies) as they have many groups in common. For a key to the species of Madagascar, which are markedly different from Africa, it is best to use the key of Ralimanana & Hoffmann (2011), which includes all morphological exceptions to the various (sub)genera. Adjustments need to be considered as some of the subgenera treated for the flora of Madagascar (Ralimanana & Hoffmann 2011, 2014, Ralimanana *et al.* 2013, Ralimanana & Cable 2020) are now in separate genera.

The most difficult groups to recognize are the same ones that provide identification issues in their current state. These are the species with a herbaceous or subshrub habit, a character that has evolved several times. This problem is exacerbated by the fact that many of these herbs have become invasive and have become pantropical.

Africa

1. Branching non-phyllanthoid (laminate leaves and flowers on all axes; branchlets not deciduous)....2
1. Branching phyllanthoid (leaves on main stem reduced to scales, the cataphylls; laminate leaves and flowers on lateral axes; lateral branchlets deciduous) or sub-phyllanthoid (leaves at base of branchlets not reduced to scales (often in juveniles); lateral branchlets deciduous)....8

2. Stamens > 10 .... *Lingelsheimia*
2. Stamens 2–7....3

3. Pistillode present in staminate flowers .... *Flueggea*
3. Pistillode absent in staminate flowers 4

4. Leaves on all axes spirally arranged....5
4. Leaves on all axes distichous 6

5. Sepals 5; stamens 5, filaments free.... *Kirganelia* section *Pseudomenarda*
5. Sepals 5–6; stamens usually 3 (sometimes 2 or 4), filaments connate…. *Nellica*

6. Sepals 4 in both sexes; staminate disc entire; stamens 4, filaments free; seeds with blue sarcotesta .... *Margaritaria*
6. Sepals 5 or 6 (4 in staminate flowers of *C. ussuriensis* and *C. petraeus*, but then 2 stamens in staminate flowers and 6 sepals in pistillate flowers); staminate disc entire or segmented; stamens 2 or 3, filaments free or connate; seeds with no or whitish sarcotesta 7

7. Sepals 4–6, staminate disc segmented, stamens 2 (but then staminate sepals 4) or 3 .... *Cathetus*
7. Sepals 6, staminate disc entire, stamens 2 .... *Plagiocladus*

8. Stamens 4–6, filaments free or partly fused (2 free, 3 fused)....9
8. Stamens usually 3, filaments connate....11

9. Herbs or subshrubs, filaments free .... *Moeroris*
9. Shrubs, sometimes climbing, to small trees, filaments free or fused in two sets 10

10. Stamens 2–5; filaments free; fruits inflated capsules or drupaceous (apple-like) .... *Cicca* subgenus *Cicca*
10. Stamens 5; filaments outer 2 free, inner 3 fused in a central column); fruits baccate.... *Kirganelia*

11. Pistillate inflorescences on proximal position and staminate inflorescences on distal position of plagiotropic branchlets; seeds transversely ribbed—ovary covered with tubercles .... *Emblica* (*E. urinaria*)
11. Pistillate inflorescences on distal position and staminate inflorescences on proximal position of plagiotropic branchlets; seeds longitudinally or transversely striate, but not ribbed.... *Moeroris*

Asia (India to Southeast Asia), Australia and Pacific

1. Branching non-phyllanthoid (laminate leaves and flowers on all axes; branchlets not deciduous) or sub-phyllanthoid (leaves at base of branchlets not reduced to scales (often in juveniles); lateral branchlets caducous)....2
1. Branching phyllanthoid (leaves on main stem reduced to scales, the cataphylls; laminate leaves and flowers on lateral axes; lateral branchlets caducous) 7

2. Disc absent.... *Synostemon*
2. Disc present 3

3. Pistillode present in staminate flowers .... *Flueggea*
3. Pistillode absent in staminate flowers 4

4. Leaves on all axes spirally arranged; filaments connate; pistillate disc segmented ..... *Nellica*
4. Leaves on all axes distichous; filaments free or connate; pistillate disc usually entire (when segmented then filaments free, except in *Cathetus womerleyi* and *Cathetus ussuriensis*) 5

5. Sepals 4 in both sexes; staminate disc entire; stamens 4, filaments free; seeds with blue sarcotesta ..... *Margaritaria*
5. Sepals 5 or 6 (4 in staminate flowers of *Cathetus ussuriensis*, but then only 2 stamens in staminate flowers and 6 sepals in pistillate flowers); staminate disc segmented (urceolate in *Cathetus gracilis* (Hassk.) R.W.Bouman); stamens 2 or 3, filaments free or connate; seeds with no or whitish sarcotesta 6

6. Branchlets not caducous; stipule base mostly auriculate; filaments free or connate, anther connective not enlarged; seeds smooth or longitudinally verrucate ..... *Cathetus*
6. Branchlets caducous; stipule base truncate; filaments free, anther connective often enlarged; seeds smooth or transversely striate. ..... *Lysiandra*

7. Disc absent 8
7. Disc present 11

8. Flowers without sepal scales; anthers sometimes apiculate; stigmas usually entire; ovary 3–15-locular 9
8. Flowers often with sepal scales; anthers not apiculate; stigmas usually bifid; ovary 3-locular 10

9. Staminate sepals spreading or tubular; filaments free; ovary 3–5-locular ..... *Dendrophyllanthus*
9. Staminate sepals often recurved; filaments connate; ovary 3–15-locular ..... *Glochidion*

10. Sepal scales often present in staminate flowers; fruits wider than long; seeds smooth ..... *Breynia*
10. Sepal scales absent in staminate flowers (except in *S. bacciformis*); fruits longer than wide; seeds sculptured ..... *Synostemon*

11. Herbs or subshrubs 12
11. Shrubs to trees, rarely climbers 14

12. Pistillate inflorescences on proximal position and staminate inflorescences on distal position on plagiotropic branchlets; seeds transversely ribbed—ovary often covered with tubercles ..... *Emblica*
12. Pistillate inflorescences on distal position and staminate inflorescences on proximal position of plagiotropic branchlets; seeds longitudinally or transversely striate, but not ribbed 14

13. Cataphyllary stipules (unilaterally) auriculate; filaments connate ..... *Moeroris*
13. Cataphyllary stipules not auriculate; filaments free ..... *Phyllanthus*

14. Sepals 4 in staminate flowers; stamens 2, filaments connate, anthers dehiscing horizontally (except in *Nym. ruber* & *Nym. touranensis*)—pollen pantoporate or clypeate ..... *Nymphanthus*
14. Sepals 5 or 6 in staminate flowers (4 in *Cicca acida*, but then stamens 4, filaments free); stamens 3–15, filaments free or connate, anthers dehiscing mostly vertically, sometimes horizontally 15

15. (Climbing) shrubs; inflorescences axillary or on specialized leafless branchlets; stamens 2 or 5, filaments free or fused in two sets (outer 2 free, inner 3 united), connectives not apiculate; fruits baccate ..... *Kirganelia*
15. (Climbing, but then stamens 3 and connate) shrubs to trees; inflorescences axillary or on specialized leafless branchlets (then stamens 3 or 4); stamen 3–20 (when 5 then inflorescences axillary, fruits capsules), filaments free or connate, but not in sets, connectives sometimes apiculate; fruits capsules or drupaceous (baccate in *Cicca pinnata* and *C. orientalis*, but then stamens 6) 16

16*. Branchlets pinnatiform; inflorescences axillary or on separate leafless plagiotropic axes; stamens 4 (in *C. acida*) or 6 (in *C. Pinnata* and *C. orientalis*), filaments free; fruits baccate (spherical <2 cm in diam. in *C. pinnata* and *C. orientalis*; star-shaped in *C. accida*) ..... *Cicca*
16*. Branchlets (bi-)pinnatiform; inflorescences axillary or sometimes paniculate; sepals 4–6; staminate disc segmented, 4–6 or 3 bilobed segments; stamens mainly 3 or 5, (in some species up to 20), filaments free (when connate then stamens 3, disc of 3 bilobed segments); stigmas entire, rarely bifid; fruits capsules ..... *Dendrophyllanthus*
16*. Branchlets pinnatiform; inflorescences axillary on leafy plagiotropic branches (floriferous branchlets sometimes with smaller leaves); sepals (4)5 or 6; staminate disc of 5 or 6 glands; stamens 3 or 4, filaments connate; stigmas mostly bifid; fruits (inflated) capsules (except in *Emblica officinalis*, there spherical drupe 2–3 cm in diam.) 17

17. (Climbing) shrubs to trees; floriferous branchlets sometimes with smaller leaves, *Glochidion* subg. *Phyllanthodendron*); stamens 3 or 4, connectives apiculate; pistillate disc segmented, segments linear; fruits (inflated) capsules .... *Glochidion* (subgenera *Phyllanthodendron* & *Pseudoactephila*)
17. Shrubs to trees; all branches with same size of leaves; stamens 3, connectives apiculate or not; pistillate disc entire; fruits capsules (drupaceous in *Emblica officinalis*) 18

18. Sepals 6; anthers dehiscing vertically, connectives often apiculate; fruits capsules (drupaceous in *E. officinalis*) ..... *Emblica*
18. Sepals 5 or 6; anthers dehiscing obliquely to horizontally, connectives not apiculate; fruits capsules ..... *Moeroris*

Americas (North America, Central America, South America) & West Indies

1. Branching non-phyllanthoid (laminate leaves and flowers on all axes; branchlets not deciduous) or sub-phyllanthoid (leaves at base of branchlets not reduced to scales (often in juveniles); lateral branchlets deciduous) 2
1. Branching phyllanthoid (leaves on main stem reduced to scales, the cataphylls; laminate leaves and flowers on lateral axes; lateral branchlets deciduous) 6

2. Pistillode present in staminate flowers 3
2. Pistillode absent in staminate flowers 4

3. Petals absent; fruits with 2 seeds per locule; pollen exine verruculose .... *Flueggea*
3. Petals present; fruits with 1or 2 seeds per locule; pollen exine reticulate .... *Heterosavia*

4. Sepals 4 in both sexes; staminate disc entire; stamens 4, filaments free; seeds with blue sarcotesta .....*Margaritaria* (Pantropical)
4. Sepals 5 or 6 in both sexes (sometimes 4 in staminate flowers, but then 2 stamens); staminate disc entire (H-shaped with 2 stamens); stamens usually 3, filaments free or connate; seeds with no or whitish sarcotesta....5

5. Leaves on all axes spirally arranged; sepals 4 in staminate flowers, 6 in pistillate flowers; staminate disc entire, H-shaped around filaments; stamens 2, filaments free .....*Moeroris* (*M. arenaria*)
5. Leaves on all axes distichous or spiral; sepals 5 or 6 in both sexes; staminate disc segmented or entire (but then filaments connate), never H-shaped; stamens 2, 3 or 5 (when 2 then filaments connate), filaments free or connate .....*Phyllanthus*

6. Herbs or subshrubs 7
6. Shrubs to trees, rarely climbers 12

7. Inflorescences unisexual....8
7. Inflorescences bisexual....11

8. Pistillate inflorescences on proximal position and staminate inflorescences on distal position of plagiotropic branchlets; seeds transversely ribbed—ovary often covered with tubercles ..... *Emblica urinaria* (Pantropical, but origin Asia)
8. Pistillate inflorescences on distal position and staminate inflorescences on proximal position of plagiotropic branchlets; seeds smooth or longitudinally or transversely striate, but not ribbed 9

9. Cataphyllary stipules not auriculate .....*Phyllanthus*
9. Cataphyllary stipules (unilaterally) auriculate....10

10. Inflorescences unisexual or bisexual; filaments connate, anthers free; seeds smooth or longitudinally striate.....*Moeroris*
10. Inflorescences usually unisexual; filaments usually free, sometimes connate, anthers free or connate in a synandrium; seeds smooth, striate or verrucate .....*Phyllanthus*

11. Stamens 2 or 3, filaments entirely or partially connate (free in *M. arenaria*), anthers dehiscing oblique to horizontally (vertically in *M. arenaria*); pistillate disc entire; pollen 3-colporate, exine reticulate; seeds smooth or longitudinally striate—North America, pantropical invasive.....*Moeroris* subgenus *Swartziani*
11. Stamens 3, filaments free, anthers dehiscing horizontally; pistillate disc segmented; pollen grains brevicolporate and diorate or porate, exine pilate; seeds verruculose —South America ..... *Phyllanthus* subgenus *Conami* section *Apolepsis*

12. Inflorescences axillary fascicles on specialized leafless branchlets or cauliflorous; staminate disc absent; stamens 3 or 4, filaments free (3, filaments connate in *C. pseudocicca*); ovary 2- or 3-locular; fruits baccate; seeds without sarcotesta…..... *Cicca*
12. Inflorescences axillary fascicles, sometimes paniculate; staminate disc present; stamens 2–15, filaments free or connate; ovary 3–6-locular; fruits baccate (inflorescences then shortly stalked) or capsules; seeds with or without sarcotesta .....*Phyllanthus*

Clade A—Figs. 1, 2A (supplementary fig. 1)

Nellica Raf.

Nellica Rafinesque (1838: 92).—Type: *Nellica maderaspatensis* (Linnaeus 1753: 982) Raf. (‘*maderaspatana*’, based on *Phyllanthus maderaspatensis* L.).

Maschalanthus Nuttall (1837: 175), nom. illeg., non *Maschalanthus* Sprengel ex Schultz (1806: 356).—*Andrachne* L. section *Maschalanthus* (Nutt.) Pax (1890: 15).—*Savia* Willd. section *Maschalanthus* (Nutt.) Pax & Hoffmann (1922: 183).—Lectotype (designated by Webster 1970): *Maschalanthus polygonoides* (Nutt. ex Sprengel 1826: 23) Nuttal (1837: 175) (based on *Phyllanthus polygonoides* Nutt. ex Spreng.) = *Nellica polygonoides* (Nutt. ex Spreng.) R.W.Bouman.

Phyllanthus Linnaeus subgenus *Isocladus* Webster (1956: 345); (1970: 55); Brunel (1987: 317); Ralimanana & Hoffmannn (2011: 334).—*Phyllanthus* L. section *Paraphyllanthus* Müller (1863: 3); (1866: 355); Bentham (1873: 94); Hooker (1887: 285); Boerlaage (1900:

213); Webster (1956: 345); (1997: 209).—*Phyllanthus* L. section *Isocladus*: Brunel (1987: 318).—Type: *Phyllanthus maderaspatensis* Linnaeus = *Nellica maderaspatensis* (L.) Rafinesque ('*maderaspatana*').

Diagnostic features: Herbs or subshrubs, monoecious, branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* spirally arranged on all axes. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 6; disc glands 6, alternating with sepals; stamens 3, filaments connate, anthers dehiscing longitudinally, vertically, connectives not apiculate, not fused; pollen prolate, 3-colporate, colpi monoporate, exine reticulate; pistillode absent. *Pistillate flowers*: sepals 6; disc glands 6, alternating with sepals; ovary 3-locular; style present; stigmas apicallly bifid. *Fruits* capsules. *Seeds* trigonous, verrucate along longitudinal rows.

Distribution: Mainly Africa, Central and North America (USA and Mexico), with one widespread species occurring in Asia and Australia.

Notes—1. *Phyllanthus maderaspatensis* L. of subgenus *Isocladus* G.L.Webster was found to be sister to all other species of *Phyllanthus* (Kathriarachchi *et al.* 2006), while the other species included in subgenus *Isocladus* were present in other clades (as far as they were included in any analysis) and classified in other subgenera/sections. Subsequently, subgenus *Isocladus* was described as monotypic (Ralimanana & Hoffmann 2011), but the *P. maderaspatensis* clade was found to also include the American species *P. polygonoides* (Bouman *et al.* 2021; supplementary fig. 1) and African *P. mendoncae* Jean F.Brunel. This shows that *Phyllanthus* subgenus *Isocladus* was not monotypic, but was merely the result of incomplete taxon sampling by Kathriarachchi *et al.* (2006). The species placed by Brunel (1987) and Webster (2001b) in the same section as *P. maderaspatensis* should be retained as one group, which is here split from *Phyllanthus* as the separate genus *Nellica*. Unfortunately, the Mexican species of section *Paraphyllanthus* (sensu Webster 2001b) was not included in any phylogenetic study and should be further investigated. Two species by Radcliffe-Smith (1996) are also included on account of their general resemblance to *Nel. maderaspatensis* (pistillate disc consisting of free glands in the drawing, and spirally arranged leaves), but they need to be further evaluated.

2. The most important characters here are the spirally arranged leaves, non-phyllanthoid branching, the connate stamens with free connectives and a segmented pistillate disc. No further subgeneric groups are currently defined for this genus, but there may be differences between the neotropical and palaeotropical species.

Included species and taxonomic changes (20 spp.):

Nellica barbarae (Johnston 1986: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus barbarae* M.C.Johnst.

Nellica caraculiensis (Brunel 1987: 320) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caraculiensis* Jean F.Brunel.

Nellica cunenensis (Brunel 1987: 320) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cunenensis* Jean F.Brunel.

Nellica ericoides (Torrey 1859: 193) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ericoides* Torr.

Nellica fraguensis (Johnston 1985: 300) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fraguensis* M.C.Johnst.

Nellica galeottiana (Baillon 1860: 32) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus galeottianus* Baill.

Nellica gypsicola (McVaugh 1961: 194) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gypsicola* McVaugh.

Nellica incurva (Thunberg 1794:) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus incurvus* Thunb.

Nellica karibibensis (Brunel 1987: 323) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus karibibensis* Jean F.Brunel.

Nellica liebmanniana (Müller1866: 366) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus liebmannianus* Müll.Arg.

Nellica maderaspatensis (Linnaeus 1753: 982) Raf. (1838: 92, as '*maderaspatana*'). Basionym: *Phyllanthus maderaspatensi*s L.

Nellica mendoncae (Brunel 1987: 324) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mendoncae* Jean F.Brunel.

Nellica neoleonensis (Croizat 1943b: 14) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus neoleonensis* Croizat.

Nellica paxianus (Dinter 1926: 379) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus paxianus* Dinter.

Nellica peninsularis (Brandegee 1899: 8) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus peninsularis* Brandegee.

Nellica polygonoides (Nutt. ex Sprengel 1826: 23) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus polygonoides* Nutt. ex Spreng.

Nellica revaughanii (Coode 1978: 120) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus revaughanii* Coode.—*Phyllanthus longifolius* Lam. ex Poir. *in* de Lamarck (1804:303), nom. illeg., non *Phyllanthus longifolius* Jacquin (1797: 36).

Nellica serpentinicola (Radcliffe-Smith 1996: 320) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus serpentinicola* Radcl.-Sm.

Nellica spinosa (Chiovendi 1929: 305) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus spinosus* Chiov.

Nellica tener (Radcliffe-Smith 1996: 323) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tener* Radcl.-Sm.

Clade B—Figs. 1, 2B & C (supplementary fig. 1)

Cathetus Lour.

Cathetus de Loureiro (1790: 608).—*Phyllanthus* L. section *Cluytiopsis* Müller (1863: 3).—*Phyllanthus* section *Cathetus* (Lour.) Müller (1866: 350), nom. superfl.; Pax (1890: 20); Pax & Hoffman (1931: 64).—Type: *Cathetus fasciculata* Lour. (= formerly *Phyllanthus cochinchinensis* Spreng.).

Diagnostic features: Herbs, subshrubs to trees, monoecious or dioecious; branching non-phyllanthoid. *Leaves* distichous or in small whorls. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 6 (except 5 in *C. aoraiensis* and usually 4 in *C. petraeus* and *C. ussuriensis*); disc glands free (urceolate in *C. gracilis*), same number as and alternating with sepals; stamens 3 (2 in *C. petraeus* and sometimes *C. ussuriensis*), filaments free or connate (connectives also fused in subgenus *Cathetus*), anthers globular or elongate, non-apiculate, dehiscing horizontally to vertically; pollen spheroidal to ellipsoidal, clypeate with colpi anastomosing around exine shields or pantoporate or peribrevicolporate without distinct colpi, exine (macro)reticulate; pistillode absent. *Pistillate flowers*: sepals 6; disc entire or consisting of free glands alternating with sepals; ovary 3-(rarely 4-)locular; styles present or absent; stigmas 3, with bifid tips. *Fruits* capsules. *Seeds* trigonous, smooth or verrucate with verrucae either random or in longitudinal lines.

Distribution: Africa, mainland Asia, Malesia, Australia and Pacific.

Note—As defined here, the reinstated genus *Cathetus* includes two subgenera that correspond to *Phyllanthus* subgenus *Macraea* (Wight) Jean F.Brunel and *Phyllanthus* subgenus *Ceramanthus* (Hassk.) Jean F.Brunel. Though previously only a section within *Phyllanthus*, *Cathetus* is the oldest name at generic level and therefore has priority over the other two names, *Macraea* and *Ceramanthus*. Subgenus *Ceramanthus* is synonymized with subgenus *Cathetus* and all its sections are here subsumed except for section *Ebolowani*, which is placed in the genus *Cicca* (discussed below). Both subgenera are characterized by non-phyllanthoid branching with usually distichous leaves in higher nodes and six sepals in the flowers with three stamens in the staminate flower. Distinctions are discussed below.

Cathetus Lour. subgenus **Cathetus**

Cathetus Lour. subgenus *Cathetus*: Literature and type as under the genus.

Ceramanthus Hasskarl (1844: 240), non *Aploca* section *Ceramanthus* Hooker ex Post & Kuntze (1903: 39), nor *Ceramanthus* (Kuntze) Malme (1905: 2).—*Phyllanthus* L. section *Ceramanthus* (Hassk.) Baillon (1858: 629); Müller (1866: 350); Pax (1890: 20); Brunel (1987: 408).—*Phyllanthus* L. subgenus *Ceramanthus* (Hassk.) Brunel (1987: 407).—Type: *Ceramanthus gracilis* Hassk. (= formerly *Phyllanthus albidiscus* (Ridl.) Airy Shaw) = *Cathetus gracilis* (Hassk.) R.W.Bouman.

Phyllanthus L. section *Anisolobium* Müller (1864: 330); Pax (1890: 20); Pax & Hoffmann (1921: 27); (1931: 63); Webster (1997: 217).—*Phyllanthus* L. subgenus *Ceramanthus* (Hassk.) Jean F.Brunel section *Anisolobium* (Müll.Arg.) Brunel (1987: 412).—Type: *Phyllanthus welwitschianus* Müll.Arg. = *Cathetus welwitschianus* (Müll.Arg.) R.W.Bouman.

Phyllanthus L. section *Bivia* Brunel & Roux (1985: 241).—*Phyllanthus* L. subgenus *Ceramanthus* (Hassk.) Jean F.Brunel section *Bivia* (Jean F.Brunel & Jacq.Roux) Brunel (1987: 414).—Type: *Phyllanthus petraeus* A.Chev. & Beille ex Beille = *Cathetus petraeus* (A.Chev. & Beille ex Beille) R.W.Bouman.

Diagnostic features: Shrubs, monoecious or dioecious. *Leaves* distichous or in small whorls. *Inflorescences* axillary, unisexual or (rarely) bisexual fascicles. *Staminate flowers*: sepals 6 (4 in *C. petraeus*); disc glands free (urceolate in *C. gracilis*), same number as and alternating with sepals; stamens 3 (2 in *C. petraeus*), filaments and connectives fused into an androphore; anthers elongate; pollen pantoporate or peribrevicolporate, colpi indistinct, exine macroreticulate. *Pistillate flowers*: sepals 6; disc entire; styles present; stigmas 3 with bifid tips. *Fruits* capsules. *Seeds* trigonous, verrucate with verrucae either random or in longitudinal lines.

Distribution: Africa and mainland Asia, Malesia (Java).

Notes—1. The main difference between subgenus *Cathetus* (formerly *Phyllanthus* subgenus *Ceramanthus*) and subgenus *Macraea* is found in the fusion of the filaments and connectives. Usually the flowers are larger and have two clear dimorphic sepal whorls in *Cathetus* subgenus *Cathetus*.

2. Three sections were recognized in *Phyllanthus* subgenus *Ceramanthus* with little taxonomic value and they are here all subsumed into subgenus *Cathetus*.

3. Pantoporate pollen also occurs in *Nymphanthus*, but they differ in the shape of the apertures (elliptic in *Cathetus*, circular in *Nymphanthus*; Wu *et al.* 2016).

Included species and taxonomic changes (6 spp.):

Cathetus binhii (Thin 1995: 48) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus binhii* Thin.

Cathetus fasciculata de Loureiro (1790: 608), homotypic synonym: *Phyllanthus cochinchinensis* Spreng. (1826: 21).

Cathetus gracilis (Hasskarl 1844: 240) R.W.Bouman, *comb. nov.* Basionym: *Ceramanthus gracilis* Hassk., non *Phyllanthus gracilis* Roxburgh (1832: 654), heterotypic synonym: *Phyllanthus albidiscus* (Ridl.) Airy Shaw (1969: 26).

Cathetus kerstingii (Brunel 1985: 251) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kerstingii* Jean F.Brunel.

Cathetus petraeus (Chevalier & Beille ex Beille 1908: 58) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus petraeus* A.Chev. & Beille ex Beille.

Cathetus welwitschianus (Müller 1864: 330) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus welwitschianus* Müll.Arg.

Cathetus Lour. subgenus **Macraea** (Wight) R.W.Bouman, *comb. nov*.

Macraea Wight (1852: 27), nom. illeg., non *Macraea* Lindley (1828:104), nec Hooker (1846: 209).—*Phyllanthus* L. section *Macraea* (Wight) Baillon (1858: 628); Müller (1866: 384); Webster (1986: 93); (1997: 211).—*Phyllanthus* L. subgenus *Macraea* (Wight) Brunel (1987: 293).—Lectotype (designated by Webster 1986): *Macraea oblongifolia* Wright (= formerly *Phyllanthus virgatus* G.Forst.) = *Cathetus simplex* (Retz.) R.W.Bouman.

Diagnostic features: Herbs, subshrubs to trees, monoecious or dioecious; branching non-phyllanthoid. *Leaves* distichous. *Inflorescences* axillary, unisexual or (rarely) bisexual fascicles. *Staminate flowers*: sepals 6 (except 5 in *C. aoraiensis* and usually 4 in *C. ussuriensis*); disc glands free, same number as and alternating with sepals; stamens 3 (sometimes 2 in *C. ussuriensis*), filaments free, sometimes connate, anthers globular; pollen clypeate, colpi anastomosing around exine shield, exine reticulate. *Pistillate flowers*: sepals 6; disc entire or consisting of free glands alternating with sepals; styles mostly absent (present in *C. ridsdalei* and *C. tenuipes*); stigmas 3 with bifid tips. *Fruits* capsular. *Seeds* trigonous, smooth or verrucate with verrucae either random or in longitudinal lines.

Distribution: Africa, mainland Asia, Malesia, Australia and Pacific.

Note—The staminate flowers of subgenus *Macraea* can be quite similar to the genus *Lysiandra* (F.Muell.) R.W.Bouman, I.Telford & J.J.Bruhl or *Phyllanthus* section *Loxopodium*, but subgenus *Macraea* differs significantly in its pollen. Species of subgenus *Macraea* can also be distinguished from *Lysiandra* by their (usually) bicolored auriculate stipules. This group has recently been revised while still in the genus *Phyllanthus* (Verwijs *et al.*, 2019), but some species are reinstated and transferred here (e.g., *C. beckleri* (Müll.Arg.) I.Telford & J.J.Bruhl, *C. filicaulis* (Benth.) I.Telford & J.J.Bruhl and *C. simplex* (Retz.) R.W.Bouman).

Included species and taxonomic changes (34 spp.):

Cathetus aoraiensis (Nadeaud 1873: 73) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aoraiensis* Nadeaud.

Cathetus beckleri (Müller 1865b: 74) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Phyllanthus beckleri* Müll.Arg.

Cathetus brevipes (Hooker 1887: 297) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus brevipes* Hook.f.

Cathetus chrysanthus (Baillon 1862b: 238) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chrysanthus* Baill.

Cathetus clarkei (Hooker 1887: 297) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus clarkei* Hook.f.

Cathetus distichus (Hooker & Arnott 1832: 95) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus distichus* Hook. & Arn.

Cathetus dumosus (Robinson 1909: 79) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dumosus* C.B.Rob.

Cathetus everettii (Robinson 1909: 80) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus everettii* C.B.Rob.

Cathetus exilis (Moore 1926: 97) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus exilis* S.Moore.

Cathetus filicaulis (Bentham 1873: 111) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Phyllanthus filicaulis* Benth.

Cathetus gardnerianus (Wight 1852: 27) R.W.Bouman, *comb. nov.* Basionym: *Macraea gardneriana* Wight, synonym: *Phyllanthus gardnerianus* (Wight) Baill. (1858: 628).

Cathetus glaucophyllus (Sonder 1850: 133) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus glaucophyllus* Sond.

Cathetus hakgalensis (Thwaites ex Trimen 1885: 242) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hakgalensis* Thwaites ex Trimen.

Cathetus lanceifolius (Merrill 1914: 489) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lanceifolius* Merr.

Cathetus minutiflorus (Mueller ex Müller 1865b: 75) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus minutiflorus* F.Muell. ex Müll. Arg.

Cathetus myrtifolius (Wight 1852: 27) R.W.Bouman, *comb. nov.* Basionym: *Macraea myrtifolia* Wight., homotypic synonym: *Phyllanthus myrtifolius* (Wight) Müller (1866: 396).

Cathetus narayansamii (Gamble 1925: 329) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus narayansamii* Gamble.

Cathetus pacificus (Müller 1863: 31) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pacificus* Müll.Arg.

Cathetus parvifolius (Buchanan-Hamilton ex Don 1825: 63) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus parvifolius* Buch.-Ham. ex D.Don.

Cathetus praetervisus (Müller 1865b: 73) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus praetervisus* Müll.Arg.

Cathetus prominulatus (Hunter & Bruhl 1997b: 153) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus prominulatus* J.T.Hunter & J.J.Bruhl.

Cathetus pseudoparvifolius (Mitra & Sanjappa 2003:10) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pseudoparvifolius* R.L.Mitra & Sanjappa.

Cathetus rheedei (Wight 1852: 27) R.W.Bouman, *comb. nov.* Basionym: *Macraea rheedei* Wight (non *Phyllanthus rheedei* Wight), homotypic synonym: *Phyllanthus macraei* Müller (1863: 29).

Cathetus ridsdalei (R.W.Bouman & Verwijs *in* Verwijs *et al.* 2019: 245) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ridsdalei* R.W.Bouman & Verwijs.

Cathetus samarensis (Müller 1865b: 73) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus samarensis* Müll.Arg.

Cathetus sanjappae (Chakrabarty & Gangopadhyay 1993: 69) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sanjappae* Chakrab. & M.Gangop.

Cathetus simplex (Retzius 1789: 29) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus simplex* Retz.

Cathetus stylosus (Griffith 1848: 33) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus stylosus* Griffith, synonym *Phyllanthus griffithii* Müller 1863: 27.

Cathetus tenuipes (Robinson 1909: 78) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuipes* C.B.Rob.

Cathetus urceolatus (Baillon 1862b: 239) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus urceolatus* Baill.

Cathetus ussuriensis (Ruprecht & Maximowicz 1857: 222) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ussuriensis* Rupr. & Maxim.

Cathetus virgatus (Forster 1786: 65) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus virgatus* G.Forst.

Cathetus wheeleri (Webster 1995: 266) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus wheeleri* G.L.Webster.

Cathetus womersleyi (Airy Shaw & Webster *in* Webster & Airy Shaw1971: 86) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus womersleyi* Airy Shaw & G.L.Webster.

Clade C—Figs. 1, 2D,E & F (supplementary fig. 1)

Kirganelia A.Juss.

Kirganelia de Jussieu (1789: 387); (1824: 108); Rafinesque (1838: 92); Baillon (1858: 611, 614); (1862b: 231); Das (1940: 158).—*Phyllanthus* L. subgenus *Kirganelia* (A.Juss.) Kurz (1873: 238); Webster (1957: 51); (1970: 62); Brunel (1987: 263).—*Phyllanthus* L. section *Kirganelia* (A.Juss.) Müller (1863: 2, 11); (1866: 341); Bentham (1873: 94); Boerlaage (1900: 212); Brunel (1987:271).—*Phyllanthus* L. section *Typhophyllanthus* Kuntze subsection *Kirganelia* (A.Juss.) Kuntze in Post & Kuntze (1904: 434).—Type: *Kirganelia phyllanthoides* Desf. ex A.Juss. (= formerly part of synonymy of *Phyllanthus casticum* P.Willemet) = *Kirganelia castica* (P.Willemet) R.W.Bouman.

Diagnostic features: Shrubs (sometimes scandent) or trees, monoecious or dioecious, branching phyllanthoid (except in section *Pseudomenarda*), branchlets pinnatiform, often fasciculate on brachyblasts. *Brachyblasts* present. *Cataphyllary stipules* triangular, sometimes spinescent, indurate, base not auriculate. *Cataphylls* triangular, often spinescent, laminate leaves in section *Pseudomenarda*. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, sometimes on separate leafless branchlets. *Staminate flowers*: sepals 4 or 5; disc glands 4 or 5, alternating with sepals; stamens 2, 5 or 6, filaments free (in subsumed section *Hemicicca* (Baill.) Müll.Arg.) or connate, often of unequal length and in 2 distinct sets; anthers ovate to orbicular, non-apiculate, dehiscing vertically to obliquely; pollen (oblate) spheroidal, 3-(4-)(syn)colporate or incomplete synaperturate, colpi mono- or diploporate, exine irregularly (mirco) reticulate to vermiculate or pilate; pistillode absent. *Pistillate flowers*: sepals 5 or 6; disc entire (segmented in *K. purpurea*); ovary 3–10-locular; styles absent; stigmas bifid to nearly entire, usually erect, sometimes reduced to small tips. *Fruits* baccate (capsule in *K. purpurea*). *Seeds* trigonous to plano-convex, smooth or variously sculptured.

Distribution: Africa, Madagascar, mainland Asia, Malesia and Australia.

Notes—1. As here circumscribed, the reinstated genus *Kirganelia* only consists of sections *Kirganelia* (including several former separate sections) and *Pseudomenarda* Müll.Arg. Previous sections that were included on the base of their five stamens with a different fusion type (Brunel 1987) are transferred here to the genus *Cicca*, which was shown to be phylogenetically distinct (Kathriarachchi *et al.* 2006; Bouman *et al.* 2021).

2. *Kirganelia* is sister to a clade comprising the genera *Lysiandra* and *Nymphanthus*. These three genera show major differences in flower and fruit morphology and are treated at the same rank.

3. *Kirganelia* is one of the older names, already established by Jussieu (1789), and it was recognized early because of the aberrent staminal fusion and berries. A similar type of stamen fusion can sometimes be found in *Phyllanthus* subgenus *Xylophylla* (L.) Pers. section *Orbicularia* (Baill.) Griseb., with some outer stamens appearing to be free while the central ones are fused, but here the berries are absent. Many other groups were once placed within *Kirganelia*, but are phylogenetically distinct (Kathriarachchi *et al.* 2006; Bouman *et al.* 2021). Species in the group can sometimes have the inflorescences on separate specialized leafless branchlets, similar to those found in the genus *Cicca*. Other similarities and differences between *Kirganelia* and *Cicca* subgenus *Anesonemoides* (Jean F.Brunel) R.W.Bouman were discussed in Ralimanana & Hoffmann (2011, 2014, under *Phyllanthus* subgenus *Kirganelia* and subgenus *Anesonemoides*). These include the presence of brachyblasts, berries and stamens fused in whorls in *Kirganelia* as opposed to brachyblasts absent and capsules and stamens mostly free in *Cicca* subgenus *Anesonemoides*.

Kirganelia A.Juss. section **Kirganelia**

Kirganelia A.Juss. section *Kirganelia*: Literature and type as under the genus.

Anisonema de Jussieu (1824: 19), nom. rej. non *Anisonema* Dujardin (1841: 344); Baillon (1858: 613).—*Phyllanthus* L. subgenus *Kirganelia* (A.Juss.) Kurz section *Anisonema* (A.Juss.) Grisebach (1859: 34); Baillon (1858: 613); (1862b: 231); Webster (1957: 56); Schmid (1991: 58).—Type: *Anisonema reticulatum* (Poir.) Jussieu (1804: 4), nom. rej. (= formerly *Phyllanthus reticulatus* Poir.) = *Kirganelia reticulata* (Poir.) Baill.

Kirganelia A.Juss. section *Anisonemopsis* Baillon (1858: 614).—Type: *Kirganelia trilocularis* Baillon (1858: 614)).—*Phyllanthus decipiens* (Baill.) Müll.Arg. f. *trilocularis* (Baill.) Leandri (= formerly *Phyllanthus casticum* P.Willemet) = *Kirganelia castica* (P.Willemet) R.W.Bouman.

Phyllanthus L. section *Flueggeopsis* Müller (1863: 2, 14); (1866: 348); Hooker (1887: 286); Boerlaage (1900: 212).—*Flueggeopsis* (Müll. Arg.) Schumann (1905: 289); Das (1940: 158).—Type: *Flueggeopsis glauca* (Wall. ex Müll.Arg.) Das (1940: 158).—*Phyllanthus glaucus* Wall. ex Müll.Arg. = *Kirganelia glauca* (Wall. ex Müll.Arg.) R.W.Bouman.

Hemicicca Baillon (1858: 645).—*Phyllanthus* L. section *Hemicicca* (Baill.) Müller (1866: 324).—*Phyllanthus* L. section *Cicca* (L.) Müll. Arg. subsection *Hemicicca* (Baill.) Müller (1863: 52).—*Glochidion* J.F.Forst. & G.Forst. section *Hemicicca* (Baill.) Pax & Hofmann (1931: 58).—Type: *Hemicicca japonica* Baill. (= formerly *Phyllanthus flexuosus* (Siebold & Zucc.) Müll.Arg.) = *Kirganelia flexuosa* (Siebold & Zucc.) R.W.Bouman.

Phyllanthus L. section *Floribundi* Pax & Hoffmann (1921: 22); Webster (1957: 51).—Type: *Phyllanthus floribundus* Müll.Arg., nom. illeg., non *Phyllanthus floribundus* Kunth, nor *Kirganelia floribunda* (Kunth) Spreng. (= formerly *Phyllanthus muellerianus* (Kuntze) Exell) = *Kirganelia muelleriana* (Kuntze) R.W.Bouman.

Phyllanthus L. subgenus *Conami* (Aubl.) G.L.Webster section *Brazzeani* Brunel & Roux, (1977: 224 (in subgenus *Conami*)); Brunel (1987: 292).—Type: *Phyllanthus dinklagei* Pax = *Kirganelia dinklagei* (Pax) R.W.Bouman.

Diagnostic features: Shrubs (sometimes scandent) or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, often fasciculate on brachyblasts. *Cataphylls* present. *Leaves* distichous. *Staminate flowers*: sepals 4 or 5; disc glands 4 or 5, alternating with sepals; stamens 5 or 6, connate, often of unequal length and in 2 distinct sets, anthers muticous, dehiscing longitudinally; pollen (oblate) spheroidal, 3-(syn)colporate or incompletely synaperturate, colpi monoporate, exine irregularly reticulate to vermiculate or pilate. *Pistillate flowers*: sepals 5 or 6; disc entire; ovary 3–10-locular; stigmas bifid to nearly unlobed. *Fruits* baccate. *Seeds* trigonous to plano-convex.

Distribution: Tropical Africa, mainland Asia, Malesia and Australia.

Notes—1. The name *Anisonema* was the first to be established on section level (Grisebach 1859), while *Kirganelia* is the older name on genus and subgeneric level. Past taxonomic treatments have often retained section *Anisonema* within *Phyllanthus* subgenus *Kirganelia* (see Webster 1958; Webster & Airy Shaw 1971; Kathriarachchi *et al.* 2006; Bouman *et al.* 2018b), but sometimes changed this in favor of section *Kirganelia* (Webster 1960; Airy Shaw 1980a). Here, with the reinstatement of the genus *Kirganelia*, the autonym rule applies and it becomes section *Kirganelia*.

2. Four sections are combined to form section *Kirganelia*. Baillon (1858) created the monotypic section *Anisonemopsis*, which was synonymized by Müller (1866) within section *Kirganelia*. *Phyllanthus* section *Floribundi*,

which was upheld by Webster (1957), was disentangled and split into several sections by Brunel (1987). His classification of *Kirganelia* was subsequently altered with the results from the phylogenetic studies by Kathriarachchi *et al.* (2006); changes in Ralimanana & Hoffmann (2011), Falcón *et al.* (20202) and Bouman *et al.* (2021, changes implemented here). According to Webster (2002 manuscript of Phyllanthus subgenus *Kirganelia*) species of *Phyllanthus* sections *Flueggeopsis* and *Floribundi* have caducous pistillate sepals, but this has not been studied in detail. Two sections, *Hemicicca* and *Flueggeopsis*, are also subsumed as they are nested within section *Kirganelia*.

3. *Phyllanthus glaucus* Wall. ex Müll.Arg. was synonymized with *Flueggea virosa* (Roxb. ex Willd.) Royle by Barker & van Welzen (2010) based on a specimen at Kew (most likely *Wallich 7927* (barcode K000246529)); however, *Wallich 7927* is a mixed collection of two distinct species, as determined by Chakrabarty & Balakrishnan (2018). Here the material separated from *Flueggea virosa* is transferred to *Kirganelia* (as *Kirganelia glauca* (Wall. ex Müll.Arg.) R.W.Bouman) and is probably closely related to *K. flexuosa*.

4. Meewis & Punt (1983) argued that section *Brazzeani* should probably be placed in subgenus *Kirganelia* as opposed to Brunel & Roux (1977), who wanted to place this section in *Phyllanthus* subgenus *Conami*. Similarities in pollen morphology, specifically the pilate exine, are probably convergent. Other characters such as the fusion of the androecium and the baccate fruits, are characters typical for *Kirganelia*. Retaining *Brazzeani* as a separate section would result in a paraphyletic section *Kirganelia*, therefore they are combined here.

Included species and taxonomic changes (22 spp.):

Kirganelia angavensis (Leandri 1957: 222) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus angavensis* Leandri.

Kirganelia archboldiana (Airy Shaw & Webster 1971:88) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus archboldianus* Airy Shaw & G.L.Webster.

Kirganelia baccata (Mueller ex Bentham 1873: 102) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baccatus* F.Muell. ex Benth.

Kirganelia castica (Willemet 1796: 55) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus casticum* P.Willemet.

Kirganelia ciccoides (Müller 1863: 13) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ciccoides* Müll.Arg.

Kirganelia dinklagei (Pax 1894: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dinklagei* Pax.

Kirganelia flexuosa (Siebold & Zuccarini 1845: 143) R.W.Bouman, *comb. nov.* Basionym: *Cicca flexuosa* Siebold & Zucc., homotypic synonym: *Phyllanthus flexuosus* (Siebold & Zucc.) Müll.Arg. (1866: 324).

Kirganelia fuscolurida (Müller 1866: 346) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fuscoluridus* Müll.Arg.

Kirganelia glaucina (Miquel 1861: 449) R.W.Bouman, *comb. nov.* Basionym: *Anisonema glaucinum* Miq., homotypic synonym: *Phyllanthus glaucinus* (Miq.) Müll.Arg. (1863: 13).

Kirganelia glauca (Wallich ex Müller 1863: 14) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus glaucus* Wall. ex Müll.Arg.

Kirganelia keyensis (Warburg 1891: 355) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus keyensis* Warb.

Kirganelia matitanensis (Leandri 1938: 196) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus matitanensis* Leandri.

Kirganelia microcarpa (Bentham 1861: 312) Hurusawa & Tanaka (*in* Hara 1966: 179). Basionym: *Cicca microcarpa* Benth., homotypic synonym: *Phyllanthus microcarpus* (Benth.) Müll.Arg. (1863: 51).

Kirganelia muelleriana (Kuntze 1891: 597) R.W.Bouman, *comb. nov.* Basionym: *Diasperus muellerianus* Kuntze, homotypic synonym: *Phyllanthus floribundus* Müll.Arg. (1863: 14), nom. illeg., non *Phyllanthus floribundus* Kunth (1817: 116); nec *Kirganelia floribunda* (Kunth) Sprengel (1826: 48)), homotypic synonym: *Phyllanthus muellerianus* (Kuntze) Exell (1944: 290).

Kirganelia novae-hollandiae (Müller 1866: 346) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus novae-hollandiae* Müll.Arg.

Kirganelia oligosperma (Hayata 1920: 93) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus oligospermus* Hayata.

Kirganelia ovalifolia (Forsskål 1775: 159) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ovalifolius* Forssk.

Kirganelia pervilleana Baillon (1861:50). Homotypic synonym: *Phyllanthus pervilleanus* (Baill.) Müll.Arg. (1863: 13).

Kirganelia polysperma (Schumacher & Thonning 1827: 416) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus polyspermus* Schumach. & Thonn.

Kirganelia reticulata (Poiret 1804: 298) Baillon (1858: 613). Basionym: *Phyllanthus reticulatus* Poir.

Kirganelia vieillardii Baillon (1862b: 231) (non *Phyllanthus vieillardii* Baill. 1862b: 236); homotypic synonym: *Phyllanthus deplanchei* Müll.Arg. (1863: 13).

Kirganelia zippeliana (Müller 1866: 433) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cantoniensis* Zippelius ex Spanoghe (1841: 347), nom. illeg., non *Phyllanthus cantoniensis* Horneman (1807: 29); nec *Phyllanthus cantoniensis* Schweigger (1812: 54), homotypic synonym: *Phyllanthus* zippelianus Müll.Arg. (1866: 433).

Kirganelia A.Juss. section **Pseudomenarda** (Müll.Arg.) R.W.Bouman, *comb. nov*.

Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Pseudomenarda* Müller (1864: 239); (1866: 349); Hoffmann (1931: 62); Brunel (1987: 267).—Type: *Phyllanthus purpureus* Müll.Arg. = *Kirganelia purpurea* (Müll.Arg.) R.W.Bouman.

Diagnostic features: Shrubs, monoecious, glabrous, branching non/sub-phyllanthoid. *Brachyblasts* present or absent. *Cataphylls* absent, leaves subtending branchlets not reduced. *Leaves* spiral, present on all axes. *Staminate flowers*: sepals 5; disc glands 5, free, massive, alternating with sepals; stamens 5, filaments free, anthers dehiscing longitudinally, vertically; pollen 3-(4-)colporate, colpi diploporate, sometimes monoporate, exine microreticulate. *Pistillate flowers*: sepals 5; disc entire in *K. somalensis*, segmented in *K. purpureus*; ovary 3-locular; style present; stigma tips bifid and dilated, reflexed. *Fruits* capsules. *Seeds* trigonous, smooth.

Distribution: Tropical Africa.

Note—Two species from Africa have leaves that subtend the branches and are present on all axes (Brunel 1987); the species in section *Kirganelia* have cataphylls subtending the branchlets, though juvenile plants may at first show laminate leaves (Bouman, *et al.* 2021, fig. 1).

Included species and taxonomic changes (2 spp.):

Kirganelia purpurea (Müller 1864: 329) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus purpureus* Müll.Arg.

Kirganelia somalensis (Hutchinson *in* Brown *et al.* 1912: 710) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus somalensis* Hutch.

Lysiandra (F.Muell.) R.W.Bouman, I.Telford & J.J.Bruhl, *comb. et stat. nov*.

Phyllanthus L. subgenus *Lysiandra* Mueller (1859: 108).—*Phyllanthus* L. section *Lysiandra* (F.Muell.) Webster (1978: 573).—Type: *Phyllanthus subcrenulatus* F.Muell. = *Lysiandra subcrenulata* (F.Muell.) R.W.Bouman.

Phyllanthus L. section *Antipodanthus* auct. non G.L.Webster: Webster (2002b: 290), p.p., only Australian species.

Diagnostic features: Shrubs, monoecious or dioecious, glabrous, branching (sub)phyllanthoid. *Brachyblasts* absent. *Cataphyllary stipules* triangular, membranous, base auriculate. *Cataphylls* if present triangular, leaves on penultimate axes mostly not reduced to scales. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6, alternating with sepals; stamens 3, filaments free or nearly so, connective enlarged, anthers discrete, dehiscing horizontally, connectives non-apiculate; pollen subglobose or spheroidal, 3- or 4-colporate, colpi monoporate, exine tectate-reticulate to tectate-perforate; pistillode absent. *Pistillate flowers*: sepals 5 or 6; disc shallowly cupuliform; ovary 3-locular; style present or absent; stigmas mostly bifid. *Fruits* capsules, subglobose. *Seeds* trigonous, scalariform with minute transverse striations or smooth.

Distribution: Endemic to Australia.

Notes—1. Originally this group was created for some Australian species of *Phyllanthus*. *Lysiandra* was confused with *Phyllanthus* section *Antipodanthus* G.L.Webster (Webster 1978, 2002b), but the recent phylogeny in Bouman *et al.* (2021) showed that the two groups fall in different clades. Section *Antipodanthus* is strictly neotropical and is retained here in the genus *Phyllanthus*, whilst *Lysiandra* is Australian. The group is distinct from section *Antipodanthus* and is placed at the same rank as the genera *Kirganelia* and *Nymphanthus*.

2. *Lysiandra* is difficult to distinguish from *Cathetus* subgenus *Macraea*, with which it has an overlapping distribution in Australia. However, species of *Lysiandra* can be distinguished by stipules with truncate bases and the transverse striations on the seeds (stipule base auriculate and seeds smooth or with longitudinally arranged verrucae in *Cathetus* subgenus *Macraea*). Some species also display phyllanthoid branching, which is never found in subgenus *Macraea*.

3. Webster (1978) placed *P. harrimannii* G.L.Webster in section *Lysiandra* (F.Muell.) G.L.Webster (his circumscription, different from what is presented here). This species is here treated as part of the neotropical *Phyllanthus* section *Antipodanthus*, which seems geographically more consistent.

4. Two species, *P. occidentalis* Hunter & Bruhl (1997c: 157) and *P. striaticaulis* Hunter & Bruhl (1996: 133) are not listed below to prevent unnecessary combinations as they will be synonymized in an upcoming revision of the genus *Lysiandra* (Telford unpublished manuscript).

Included species and taxonomic changes (25 spp.):

Lysiandra arida (Bentham 1873: 110) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aridus* Benth.

Lysiandra australis (Hooker 1847: 284) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus australis* Hook.f.

Lysiandra baeckeoides (Hunter & Bruhl 1997b: 149) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baeckeoides* J.T.Hunter & J.J.Bruhl.

Lysiandra calycina (Labillardière 1806: 75) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus calycinus* Labill.

Lysiandra carpentariae (Müller 1865b: 72) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carpentariae* Müll.Arg.

Lysiandra cauticola (Hunter & Bruhl 1997b: 151) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cauticola* J.T.Hunter & J.J.Bruhl.

Lysiandra collina (Domin 1927: 320) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus collinus* Domin.

Lysiandra dallachyana (Bentham 1873: 104) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dallachyanus* Benth.

Lysiandra eremica (Barrett & Telford 2015: 152) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus eremicus* R.L.Barrett & I.Telford.

Lysiandra eutaxioides (Moore 1920: 216) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus eutaxioides* S.Moore.

Lysiandra flagellaris (Bentham 1873: 106) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus flagellaris* Benth.

Lysiandra fuernrohrii (Mueller 1855: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fuernrohrii* F.Muell.

Lysiandra gunnii (Hooker 1847: 284) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gunnii* Hook.f.

Lysiandra hamelinii (Telford & Barrett 2015: 155) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hamelinii* I.Telford & R.L.Barrett.

Lysiandra hirtella (Mueller ex Müller 1863: 22) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hirtellus* F.Muell. ex Müll.Arg.

Lysiandra indigoferoides (Bentham 1873: 110) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus indigoferoides* Benth.

Lysiandra involutus (Hunter & Bruhl 1997c: 155) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus involutus* J.T.Hunter & J.J.Bruhl.

Lysiandra microclada (Müller 1865b: 71) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus microcladus* Müll.Arg.

Lysiandra oblanceolata (Hunter & Bruhl 1996: 128) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus oblanceolatus* J.T.Hunter & J.J.Bruhl.

Lysiandra savannicola (Domin 1927: 321) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus savannicola* Domin.

Lysiandra saxosa (Mueller 1853: 441) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus saxosus* F.Muell.

Lysiandra scabra (Klotzsch 1845: 179) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus scaber* Klotzsch.

Lysiandra similis (Müller 1865b: 71) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus similis* Müll.Arg.

Lysiandra subcrenulata (Mueller 1859: 108) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus subcrenulatus* F.Muell.

Lysiandra triandra (Hooker *in* Mitchell 1848: 342) R.W.Bouman, *comb. nov.* Basionym: *Micrantheum triandrum* Hook. (non *Phyllanthus triandrus* (Blanco) Müller (1865a: 379), homotypic synonym: *Phyllanthus mitchellii* Bentham (1873: 103).

Nymphanthus Lour.

Nymphanthus de Loureiro (1790: 543), non *Nymphanthus* Desvaux (1818) (latter is orthographic variant of *Nymphozanthus* Richard (1808: 63, 68, 100), nom. rej.)).—*Phyllanthus* L. section *Nymphanthus* (Lour.) Müller (1866: 419); Pax & Hoffmann (1931: 65).—Lectotype (designated by Webster 1994 and confirmed here): *Nymphanthus ruber* Lour. (as *Nymphanthus rubra* = formerly *Phyllanthus ruber* (Lour.) Spreng.).

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present or absent. *Cataphyllary stipules* triangular, indurate or membranous, base not auriculate. *Cataphylls* triangular, often slender. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles (inflorescences in *Nym. nhatrangensis* (Beille) R.W.Bouman, only subtended by a scale at proximal and distal part of branchlet with laminate leaves in the middle). *Staminate flowers*: sepals 4; disc 4 free glands, alternating with sepals; stamens 2 or 4, filaments and connectives connate, anthers globular or ovoid, dehiscing horizontally (rarely vertically), connectives non-apiculate; pollen spheroidal to ellipsoidal, pantoporate without distinct colpi, exine reticulate; pistillode absent. *Pistillate flowers*: sepals 5 or 6; disc shallowly cupuliform to urceolate or 5, rarely 6 free glands; ovary 3–8-locular; style present or absent; stigmas bifid or entire. *Fruits* capsules. *Seeds* trigonous, smooth or striate.

Distribution: Australia, mainland Asia, Malesia.

Notes—1. *Nymphanthus* is the older generic name and therefore takes priority over the names *Eriococcus* Hassk. and *Scepasma* Blume (see synonyms under the sections). This genus is split off from *Phyllanthus* and we retain two sections from the previous classifications (e.g., Müller 1866; Webster 1956). Section *Emblicastrum* Müll.Arg. is combined with section *Scepasma* to avoid paraphyly.

2. *Nymphanthus* was found to be sister to *Lysiandra* (Fig. 1), but they differ significantly in their flower morphology. Both genera have phyllanthoid branching, but the staminate flowers in *Nymphanthus* always have four sepals with two stamens. The closest resemblance is found in the neotropical *Phyllanthus chryseus* R.A.Howard, but that species differs in its entire disc in the staminate flower (Webster 1956, 1958).

3. Some previously unplaced species in Bouman *et al.* (2018) are here included in *Nymphanthus*. Several species placed by Thin (2007) in *Phyllanthus* section *Hedycarpidium* Müll.Arg. are furthermore transferred to *Nymphanthus* as this section was originally for species with tetramerous staminate flowers, which is typical for the genus. Other species from Sulawesi and the Philippines are included based on material seen digitally.

4. While *Nym. rubra* has been listed as the type for the genus *Nymphanthus* in previous publications (Webster 1994; Radcliffe-Smtih 2001), de Loureiro (1790) includes several species from which an official lectotype should have been designated. We were unable to find any formal lectotypification, so this is validated here.

Nymphanthus Lour. section **Nymphanthus**

Nymphanthus Lour. section *Nymphanthus*: Literature and type as under the genus.

Eriococcus Hasskarl (1843: 143).—*Epistylium* Sw. section *Eriococcus* (Hassk.) Baillon (1858: 648).—*Phyllanthus* L. section *Eriococcus* (Hassk.) Müller (1863: 3, 46); (1866: 420); Pax & Hoffmann (1931: 65); Webster (1997: 229).—*Phyllanthus* L. subgenus *Eriococcus* (Hassk.) Croizat & Metcalf (1942: 32); Webster (1957: 359).—Type: *Eriococcus gracilis* Hassk. (= formerly Phyllanthus gracilipes Miq.) Müll.Arg.) = *Nymphanthus gracilis* (Hassk.) R.W.Bouman

Reidia Wight (1852: 27, pls. 1903, 1904); Hooker (1887: 286); Boerlage (1900: 213); Gamble (1925) 1291); Das (1940: 155).—Lectotype (designated here, after Webster in his *Eriococcus* manuscript, 2002): *Reidia polyphylla* Wight (= formerly *Phyllanthus anabaptizatus* Müll.Arg., non *Phyllanthus polyphyllus* Willd.) = *Nymphanthus polyphyllus* (Wight) R.W.Bouman.

Phyllanthus L. section *Eriococcodes* Müller (1863: 3, 50); (1866: 419); Boerlage (1900: 213); Pax & Hoffmann (1931: 65).—Type: *Phyllanthus acutissimus* Miq. = *Nymphanthus longifolius* (Hassk.) R.W.Bouman (non *Phyllanthus longifolius* Jacquin 1797: 36).

Phyllanthus L. subgenus *Eriococcus* (Hassk.) Croizat & Metcalf section *Eriococcus* subsection *Spiciferens* Brunel (1987: 231.—Type: *Phyllanthus nhatrangensis* Beille = *Nymphanthus nhatrangensis* (Beille) R.W.Bouman.

Phyllanthus L. subgenus *Cicca* (L.) G.L.Webster section *Discofractus* Thin (1999: 49).—Type: *Phyllanthus discofractus* Croizat (formerly *Phyllanthus gracilipes* (Miq.) Müll.Arg.) = *Nymphanthus gracilis* (Hassk.) R.W.Bouman.

Phyllanthus L. subgenus *Eriococcus* (Hassk.) Croizat & Metcalf section *Eriococcus* subsection *Integra* Thin (1999: 54).—Type: *Phyllanthus rubescens* Beille. = *Nymphanthus rubescens* (Beille) R.W.Bouman.

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves*distichous. *Inflorescences* axillary, unisexual (subtended by scales in *Nym. nhatrangensis*). *Staminate flowers*: sepals 4; disc glands 4, free; stamens 2 or 4, filaments connate; anthers dehiscing horizontally (rarely vertically). *Pistillate flowers*: sepals 5 or 6; disc cupuliform; ovary 3-locular (6-locular in *Nym. ruber*); style absent; stigmas bifid. *Fruits* (inflated) capsules. *Seeds* trigonous, smooth or striate.

Distribution: Mainland Asia, Malesia and Australia.

Notes—1. *Reidia polyphylla* Wight is selected as the lectotype for the genus *Reidia* by Webster in his manuscripts (see Webster 2002 Manuscript synopsis of subgenus *Eriococcus*; typification effectively published here), because among Wight's species it has the characteristic lacerate sepals. Different type species were listed for *Reidia* in Pfeizer (1848: *Reidia tetrandra* (Roxburgh) Narayanswami) and Chakrabarty & Balakrishnan (2018: *Reidia floribunda*), which might be considered as inadvertent lectotypifications.

2. A few sections formerly retained in *Phyllanthus* subgenus *Eriococcus* are here combined with the former *Phyllanthus* section *Nymphanthus*. These are often monotypic groups that are nested within a paraphyletic section *Eriococcus*. They are combined, but can be resurrected if a full revision of the genus shows the clades to be morphologically distinct. The validity of the formerly established sections was questioned by Webster (1956, 1958), who thought that some species might only show unique character changes (autapomorphies). Thin (1999) divided *Phyllanthus* section *Eriococcus* into two subsections distinguishable based on the sepal margin (entire in *P.* subsection *Integra* Thin and fimbriate in *P.* subsection *Eriococcus*).

Included species and taxonomic changes (78 spp.):

Nymphanthus acutus (Wallich ex Müller 1865b: 75) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus acutus* Wall. ex Müll.Arg.

Nymphanthus armstrongii (Bentham 1873: 112) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus armstrongii* Benth.

Nymphanthus balakrishnanii (Sunil, Kumar & Naveen Kum *in* Sunil *et al.* 2016: 65) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus balakrishnanii* Sunil, K.M.P.Kumar & Naveen Kum.

Nymphanthus balansae (Beille 1927: 602) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus balansae* Beille.

Nymphanthus beddomei (Gamble 1925: 331) R.W.Bouman, *comb. nov.* Basionym: *Reidia beddomei* Gamble, homotypic synonym: *Phyllanthus beddomei* (Gamble) Mohanan (1985: 480).

Nymphanthus birmanicus (Müller 1863: 47) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus birmanicus* Müll.Arg.

Nymphanthus blancoanus (Müller 1863: 49) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tetrander* Blanco, nom. illeg., non *Phyllanthus tetrandrus* Roxb. (1832: 674), homotypic synonym: *Phyllanthus blancoanus* Müll.Arg.

Nymphanthus bodinieri (Léveillé 1915a: 406) R.W.Bouman, *comb. nov.* Basionym: *Sterculia bodinieri* H.Lév., homotypic synonym: *Phyllanthus bodinieri* (H.Lév.) Rehder (1937: 212).

Nymphanthus celebicus (Koorders 1898: 588, 627) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus celebicus* Koord.

Nymphanthus chantrieri (André 1883: 537) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chantrieri* André.

Nymphanthus chantaranothaii (Pornpongrungrueng, Parnell & Hodkinson *in* Pornpongrungrueng *et al.* 2019: 39) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chantaranothaii* Pornp., J.Parn. & Hodk.

Nymphanthus chekiangensis (Croizat & Metcalf 1942: 194) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chekiangensis* Croizat & Metcalf.

Nymphanthus chinensis de Loureiro (1790: 544), heterotypic synonym: *Phyllanthus villosus* Poiret (1804: 297) (non *Kirganelia villosa* Blanco (1837: 712) = *Breynia villosa* (Blanco) Welzen & Pruesapan in van Welzen *et al.* 2014: 93).

Nymphanthus daclacensis (Thin 1992: 23) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus daclacensis* Thin.

Nymphanthus elegans (Wallich ex Müller 1863: 46) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus elegans* Wall. ex Müll.Arg.

Nymphanthus evrardii (Beille 1927: 599) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus evrardii* Beille.

Nymphanthus fangchengensis (Li 1987a: 377) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fangchengensis* P.T.Li.

Nymphanthus filicifolius (Gage 1914: 241) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus filicifolius* Gage.

Nymphanthus fimbriatus (Wight 1852: 28, t. 1904 (1)) R.W.Bouman, *comb. nov.* Basionym: *Reidia fimbriata* Wight, homotypic synonym: *Phyllanthus fimbriatus* (Wight) Müller (1863: 47).

Nymphanthus fimbricalyx (Li 1987a: 380) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fimbricalyx* P.T.Li.

Nymphanthus floribundus (Wight 1852: 25, t. 1903) R.W.Bouman, *comb. nov.* Basionym: *Reidia floribunda* Wight (non *Phyllanthus floribundus* Kunth 1817: 116), homotypic synonym: *Phyllanthus cinereus* Müller (1863: 48).

Nymphanthus forrestii (Smith 1914: 195) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus forrestii* W.W.Sm.

Nymphanthus franchetianus (Léveillé 1915b: 23) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus franchetianus* H.Lév.

Nymphanthus gageanus (Gamble 1925: 331) R.W.Bouman, *comb. nov.* Basionym: *Reidia gageana* Gamble.

Nymphanthus glabrescens (Miquel 1859: 374) R.W.Bouman, *comb. nov.* Basionym: *Reidia glabrescens* Miq., homotypic synonym: *Phyllanthus glabrescens* (Miq.) Müller (1863: 48).

Nymphanthus glaucescens (Baillon ex Miquel 1859: 374) R.W.Bouman, *comb. nov.*, Basionym: *Reidia glaucescens* Miq. (non *Phyllanthus glaucescens* Kunth 1817: 115), heterotypic synonym: *Phyllanthus pulcher* Wall. ex Müll.Arg. (1863) 49. heterotypic synonym: *Phyllanthus pulcher* Wall. ex Müll.Arg. (1863) 49.

Nymphanthus gomphocarpus (Hooker 1887: 301) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gomphocarpus* Hook.f.

Nymphanthus gracilis (Hasskarl 1843: 143) R.W.Bouman, *comb. nov.* Basionym: *Eriococcus gracilis* Hassk. (non *Phyllanthus gracilis* Roxburgh 1832: 654 nor *P. gracilis* (Hassk.) Baillon 1858: 630, nom. illeg. = *P. albidiscus* (Ridley 1923: 360) Airy Shaw (1969: 26)), heterotypic synonym: *Phyllanthus gracilipes* (Miq.) Müller (1863: 47).

Nymphanthus greenei (Elmer 1910: 929) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus greenei* Elmer.

Nymphanthus guangdongensis (Li 1987a: 376) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus guangdongensis* P.T.Li.

Nymphanthus hainanensis (Merrill 1935: 20) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hainanensis* Merr.

Nymphanthus huamotensis (Pornpongrungrueng, Chantaranotha & J.Parnell *in* Pornpongrungrueng *et al.* 2019: 36) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus huamotensis* Pornp., Chantar. & J.Parn.

Nymphanthus insulensis (Beille 1927: 604) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus insulensis* Beille.

Nymphanthus kampotensis (Beille 1927: 606) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kampotensis* Beille.

Nymphanthus kinabaluicus (Airy Shaw 1974: 294) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kinabaluicus* Airy Shaw.

Nymphanthus laciniatus (Robinson 1909: 84) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus laciniatus* C.B.Rob.

Nymphanthus latifolium (Wight 1852: 28, t. 1904(2)) R.W.Bouman, *comb. nov.* Basionym: *Reidia latifolia* Wight (non *Phyllanthus latifolius* (Linnaeus 1771: 221) Swartz (1800: 1109)), synonym: *Phyllanthus baillonianus* Müller (1863: 47).

Nymphanthus leptoclados (Bentham1861: 312) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leptoclados* Benth.

Nymphanthus leytensis (Elmer 1908: 307) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leytensis* Elmer.

Nymphanthus liukiuensis (Matsumura ex Hayata 1904: 11) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus liukiuensis* Matsum. ex Hayata.

Nymphanthus longifolius (Hasskarl 1843: 143) R.W.Bouman, *comb. nov.* Basionym: *Scepasma longifolia* Hassk. (as '*longifolium*') (non *Phyllanthus longifolius* Jacquin 1797: 36), homotypic synonym: *Phyllanthus acutissimus* Miquel (1859: 369).

Nymphanthus macgregorii (Robinson 1911: 334) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus macgregorii* C.B.Rob.

Nymphanthus macrocalyx (Müller 1863: 48) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus macrocalyx* Müll.Arg.

Nymphanthus megacarpus (Gamble 1925: 332) R.W.Bouman, *comb. nov.* Basionym: *Redia megacarpa* Gamble, homotypic synonym: *Phyllanthus megacarpus* (Gamble) Kumari & Chandrabose *in* Henry *et al.* (1987: 238).

Nymphanthus megalanthus (Robinson 1911: 334) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus megalanthus* C.B.Rob.

Nymphanthus minahassae (Koorders 1898: 588, 627) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus minahassae* Koord.

Nymphanthus mindorensis (Robinson 1909: 82) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mindorensis* C.B.Rob.

Nymphanthus muriculatus (Smith 1910: 93) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus muriculatus* J.J.Sm.

Nymphanthus muscosus (Ridley 1909: 61) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus muscosus* Ridl.

Nymphanthus nanellus (Li 1987a: 376) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nanellus* P.T.Li.

Nymphanthus nhatrangensis (Beille 1927: 601) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nhatrangensis* Beille.

Nymphanthus montanum (Thwaites *in* Thwaites & Hooker 1861: 283) R.W.Bouman, *comb. nov.* Basionym: *Epistylium montanum* Thwaites (non *Phyllanthus montanus* (Sw.) Swartz 1800: 1117), homotypic synonym: *Phyllanthus oreophilus* Müller (1863: 49).

Nymphanthus ovalifolius (Wight 1852: 28, t. 1904(3)) R.W.Bouman, *comb. nov.* Basionym: *Reidia ovalifolia* Wight (non *Phyllanthus ovalifolius* Forsskål 1776: 159), homotypic synonym: *Phyllanthus heyneanus* Müller (1863: 49) (non *Phyllanthus heyneanus* (Wight 1852: pl. 1908) Müller (1865a: 389), nom. illeg. = *Glochidion heyneanum* Wight).

Nymphanthus pireyi (Beille 1927: 605) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pireyi* Beille.

Nymphanthus polyphyllus (Wight 1852: 28, t. 1904(4)) R.W.Bouman, *comb. nov.* Basionym: *Reidia polyphylla* Wight (non *Phyllanthus polyphyllus* Willdenow 1805: 586), homotypic synonym: *Phyllanthus anabaptizatus* Müller (1866: 421).

Nymphanthus pulchroides (Beille 1927: 597) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pulchroides* Beille.

Nymphanthus rangachariarii (Murugan, Kabeer & Murthy 2009: 201) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rangachariarii* Murugan, Kabeer & G.V.S.Murthy.

Nymphanthus roxburghii R.W.Bouman, *nom. nov.*, homotypic synonym: *Phyllanthus tetrandrus* Roxburgh (1832: 674) (non *Agyneia tetrandra* Buch.-Ham 1827: 125.).

Nymphanthus ruber de Loureiro (1790: 544), homotypic synonym: *Phyllanthus* ruber (Lour.) Sprengel (1826: 22 (non *Phyllanthus ruber* Noronha (1790: 22) nom. nud.).

Nymphanthus rubescens (Beille 1927: 602) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rubescens* Beille.

Nymphanthus rubristipulus (Govaerts & Radcliffe-Smith 1996: 117) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rubriflorus* Beille (1927: 600), nom. illeg., non *Phyllanthus rubriflorus* Smith (1912: 781), homotypic synonym: *Phyllanthus rubristipulus* Govaerts & Radcl.-Sm.

Nymphanthus sanatanadharmae (Mathew & Yohannana 2021: 290) R.W.Bouman, *comb. nov.* Basionym: Phyllanthus sanatanadharmae J.Mathew & Yohannan.

Nymphanthus sibuyanensis (Elmer 1910: 928) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sibuyanensis* Elmer.

Nymphanthus singalensis (Miquel 1861: 449) R.W.Bouman, *comb. nov.* Basionym: *Reidia singalensis* Miq., homotypic synonym: *Phyllanthus singalensis* (Miq.) Müller (1863: 48).

Nymphanthus singampattianus (Sebastine & Henry 1960: 437) R.W.Bouman, *comb. nov.* Basionym: *Reidia singampattiana* Sebast. & A.N.Henry, homotypic synonym: *Phyllanthus singampattianus* (Sebast. & A.N.Henry) Kumari & Chandrabose *in* Henry *et al.* (1987: 238).

Nymphanthus songboiensis (Thin 1992: 18) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus songboiensis* Thin.

Nymphanthus sootepensis (Craib 1911: 459) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sootepensis* Craib.

Nymphanthus spirei (Beille 1927: 606) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus spirei* Beille.

Nymphanthus squamifolius de Loureiro (1790: 544), homotypic synonym: *Phyllanthus squamifolius* (Lour.) Stokes (1812: 364).

Nymphanthus stipulaceus (Gamble 1925: 332) R.W.Bouman, *comb. nov.* Basionym: *Reidia stipulacea* Gamble (non *Phyllanthus stipulaceus* Bojer 1837: 280); homotypic synonym: *Phyllanthus chandrabosei* Govaerts & Radcliffe-Smith (1996: 176).

Nymphanthus stipularis (Merrill 1906: 75) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus stipularis* Merr.

Nymphanthus talbotii (Sedgwick 1921: 124) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus talbotii* Sedgw.

Nymphanthus taxodiifolius (Beille 1927: 605) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus taxodiifolius* Beille.

Nymphanthus tetrandrus (Buchanan-Hamilton 1827: 125) R.W.Bouman, *comb. nov.* Basionym: *Agyneia tetrandra* Buch.-Ham. (non *Phyllanthus tetrandrus* Roxb. 1832: 674), homotypic synonym: *Phyllanthus sikkimensis* Müll.Arg. (1863: 48).

Nymphanthus touranensis (Beille 1927: 608) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus touranensis* Beille.

Nymphanthus trichosporus (Adelbert *in* Adelbert & Meeuse 1945: 507) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus trichosporus* Adelb.

Nymphanthus triphlebius (Robinson 1909: 82) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus triphlebius* C.B.Rob.

Nymphanthus tui (Thin 1996: 48) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tui* Thin.

Nymphanthus Lour. section **Scepasma** (Blume) R.W.Bouman, comb. nov.

Scepasma Blume (1826: 582); Baillon (1858: 648); Miquel (1859: 378).—*Phyllanthus* L. section *Scepasma* (Blume) Müller (1863: 3, 50); (1866: 426); Boerlage (1900: 213); Pax & Hoffmann (1931: 65).—Type: *Scepasma buxifolia* Blume (= formerly *Phyllanthus buxifolius* (Blume) Müll.Arg.) = *Nymphanthus buxifolius* (Blume) R.W.Bouman.

Phyllanthus L. section *Emblicastrum* Müller (1866: 324).—*Glochidion* J.R.Forst. & G.Forst. section *Emblicastrum* (Müll.Arg.) Pax & Hoffmann (1931: 58).—Type: *Phyllanthus lamprophyllus* Müll.Arg. = *Nymphanthus lamprophyllus* (Müll.Arg.) R.W.Bouman.

Diagnostic features: Shrubs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present or absent. *Leaves* distichous. *Inflorescences* axillary, unisexual, flowers solitary, sessile or subsessile. *Staminate flowers*: sepals 4; disc glands 4; stamens 2, filaments connate, anthers dehiscing horizontally. *Pistillate flowers*: sepals 5, rarely 6; disc entire or 5, rarely 6 free glands; ovary (4- or) 5–8-locular; styles present or absent; stigmas usually entire (bifid in *Nym. watsonii* (Airy Shaw) R.W.Bouman). *Fruits* capsules. *Seeds* trigonous, smooth to transversely striate with small hairs.

Distribution: Malesia (Peninsular Malaysia, Java, Borneo, Philippines, Papua New Guinea) to Australia.

Note—A relatively small section accommodating a few glabrous species from Southeast Asia, mainly recognized by their staminate flowers that appear closed with erect sepals (as opposed to spreading at maturity in the rest of the genus) and usually entire stigmas. Airy Shaw (1976) discussed at length the mistake by Müller (1866) and Warburg (1894) in interpreting the stamen fusion and anther dehiscence of this section and suggested also that some of the Philippine species might be combined with *Nym. lamprophyllus* (Bouman *et al.* in prep.).

Included species and taxonomic changes (8 spp.):

Nymphanthus anisophyllaeoides (Merrill 1925: 465) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus anisophyllaeoides* Merr.

Nymphanthus balgooyi (Hoffmann & Baker in Hoffmann *et al.* 2003: 195) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus balgooyi* Petra Hoffm. & A.J.M.Baker.

Nymphanthus buxifolius (Blume 1826: 583) R.W.Bouman, *comb. nov.* Basionym: *Scepasma buxifolia* Blume, homotypic synonym: *Phyllanthus buxifolius* (Blume) Müller (1863: 50).

Nymphanthus curranii (Robinson 1909: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus curranii* C.B.Rob.

Nymphanthus lamprophyllus (Müller 1866: 324) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lamprophyllus* Müll.Arg.

Nymphanthus palauensis (Hosokawa 1935: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus palausensis* Hosok.

Nymphanthus robinsonii (Merrill 1912: 405) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus robinsonii* Merr.

Nymphanthus watsonii (Airy Shaw 1971: 493) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus watsonii* Airy Shaw.

Clade D—Figs. 1, 2I (supplementary fig. 1)

Moeroris Raf.

Moeroris Rafinesque (1838: 91).—Type: *Moeroris stipulata* Raf. (= formerly *Phyllanthus stipulatus* (Raf.) G.L.Webster).

Diagnostic features: Herbs, (sub)shrubs or small trees, monoecious or dioecious, branching (sub-)phyllanthoid (non-phyllanthoid in *M. arenaria* (A.Gray) R.W.Bouman), branchlets pinnatiform (rarely bi-pinnatiform in subgenus *Tenellanthus* (Jean F.Brunel) R.W.Bouman). *Brachyblasts* absent. *Cataphyllary stipules* triangular, usually membranous, subcoriaceous to coriaceous (just as the cataphylls), base unilaterally auriculate. *Cataphylls* triangular, rarely absent and leaves on orthotropic branches not reduced. *Leaves* distichous (or spiral). *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6 (4 in *M. arenaria*); disc glands 5 or 6, free, alternating with sepals (H-shaped in *M. arenaria*); stamens (2)3 or 5(–7 in *M. nummulariifolius* (Müll.Arg.) R.W.Bouman), filaments free or (partially) connate; anthers globular to elongate, dehiscing obliquely, vertically or horizontally, connectives non-apiculate; pollen usually 3- (or 4-)colporate, colpi monoporate, exine macro- or bireticulate, homobrochate, tectate or microperforate; pistillode absent. *Pistillate flowers*: sepals 5 or 6; disc entire or shallowly cupuliform, sometimes fringed, lobed or divided; ovary 3-locular; style absent or short; stigma tips bifid. *Fruits* capsules. *Seeds* trigonous, smooth, papillose, verrucose or longitudinally striate or banded and transversely striate or barred.

Distribution: Americas, Tropical Africa, Madagascar, few in Asia (few widely invasive species).

Note—Moeroris is the oldest generic name available for this clade, which consists of three main subgenera, *Moeroris* (formerly *Phyllanthus* subgenus *Afroswartziani*), *Swartziani* (G.L.Webster) R.W.Bouman and *Tenellanthus* (Jean F.Brunel) R.W.Bouman. These were originally placed respectively in subgenus *Phyllanthus* (being low subshrubs to herbs) and *Kirganelia* (based on the presence of five stamens). Their pollen was distinct and later it was shown that these groups were phylogenetically distinct and each was raised to subgeneric level (see Ralimanana & Hoffmann 2011, 2014). These subgenera are mainly distinguished by the either unisexual (subgenus *Moeroris* and *Tenellanthus*) or bisexual (subgenus *Swartziani*) inflorescences. The various herbs and subshrubs in this genus have often been treated with other herbaceous species in subgenus *Phyllanthus* from which they are distinguished by the staminate flower and cataphyllary stipules. Herbaceous species of the genus *Emblica* (e.g., *E. urinaria* (L.) R.W.Bouman)

can be distinguished by the same characters, but also by the organization of staminate and pistillate flowers along a branchlet.

Moeroris Raf. subgenus **Moeroris**

Moeroris Raf. subgenus *Moeroris*: Literature and type as under the genus.

Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus* subsection *Pentaphylli* Webster (1955: 54); (1957: 324); (1970: 72).—Type: *Phyllanthus pentaphylla* C.Wright ex Griseb. = *Moeroris pentaphylla* (C.Wright ex Griseb.) Falcón & R.W.Bouman.

Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus* subsection *Odontadenii* Brunel & Roux (1981: 70); Brunel (1987: 339).—*Phyllanthus* L. subgenus *Afroswartziani* Ralim. & Petra Hoffm. section *Odontadenii* (Jean F.Brunel & Jacq.Roux) Bouman in Bouman *et al.* (2018: 170).—Type: *Phyllanthus odontadenius* Müll.Arg. = *Moeroris odontadenia* (Müll.Arg.) R.W.Bouman.

Phyllanthus L. subgenus *Tenellanthus* Jean F.Brunel section *Tangani* Brunel (1987: 307).—Type: *Phyllanthus kaessneri* Hutch. = *Moeroris kaessneri* (Hutch.) R.W.Bouman.

Phyllanthus L. subgenus *Phyllanthus* section *Anthophyllus* Jean F.Brunel subsection *Callidisci* Brunel (1987: 334).—*Phyllanthus* L. subgenus *Afroswartziani* Ralim. & Petra Hoffm. section *Callidisci* (Jean F.Brunel) Bouman *in* Bouman *et al.* (2018) 169.—Type: *Phyllanthus callidiscus* Jean F.Brunel (= formerly *Phyllanthus fischeri* Pax) = *Moeroris fischeri* (Pax) R.W.Bouman.

Phyllanthus L. subgenus *Phyllanthus* section *Fluitantoides* Brunel (1987: 387).—Type: *Phyllanthus felicis* Jean F.Brunel = *Moeroris felicis* (Jean F.Brunel) R.W.Bouman.

Phyllanthus L. subgenus *Phyllanthus* section *Praephyllanthus* Brunel (1987: 389).—Type: *Phyllanthus arvensis* Müll.Arg. = *Moeroris arvensis* (Müll.Arg.) R.W.Bouman.

Phyllanthus L. subgenus *Phyllanthus* section *Microdendron* Brunel (1987: 401).—Type: *Phyllanthus microdendron* Welw. ex Müll.Arg. = *Moeroris microdendron* (Welw. ex Müll.Arg.) R.W.Bouman.

Phyllanthus L. subgenus *Afroswartziani* Ralimanana & Hoffmann in Ralimanana *et al.* (2013: 538).—Type: *Phyllanthus lokohensis* Leandri = *Moeroris lokohensis* (Leandri) R.W.Bouman.

Diagnostic features: Herbs, shrubs or small trees, almost always woody at the base, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Inflorescences* axillary, unisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6, free; stamens (2 or) 3 (variable in *M. kaessneri*), filaments partially or entirely connate, anthers dehiscing obliquely or horizontally (vertically in *M. maestrensis*); pollen (sub)prolate, 3- or 4-colporate, colpi monoporate, perihexabrevisulcate or sulcate macro- or bireticulate, tectate or microperforate. *Pistillate flowers*: sepals 5 or 6; disc entire or shallowly cupuliform, sometimes fringed, lobed or divided; ovary 3-locular; style absent; stigmas bifid, sometimes capitate. *Fruits* capsules. *Seeds* trigonous, smooth or longitudinally striate or banded and transversely striate or barred.

Distribution: Mainly tropical Africa, some species in mainland Asia and in the West Indies.

Notes—1. *Phyllanthus* subgenus *Afroswartziani* is here subsumed within the genus *Moeroris*. Subgenus *Moeroris* is differentiated from *Moeroris* subgenus *Swartziani* by its unisexual inflorescences. Both subgenera differ from *Moeroris* subgenus *Tenellanthus* in their staminate flowers, which usually have 5 or 6 sepals with 3 connate stamens (5 sepals and 5 free stamens in subgenus *Tenellanthus*).

2. Webster's unpublished manuscript (Webster 2002 synopsis of *Phyllanthus* subgenus *Phyllanthus*) describes several series for *Phyllanthus* subsection *Swartziani*, which were never formally published. Species that were included in his Neotropical *Phyllanthus* subsection *Swartziani* series *Stipulati* were placed in subgenus *Swartziani* by Bouman *et al.* (2018). However, it was shown that these species are related to other African species and are transferred here to this subgenus. The unisexual inflorescences of these species also confirms placement in subgenus *Moeroris*.

3. *Phyllanthus* sections *Callidisci* (Jean F.Brunel) R.W.Bouman, *Fluitantoides* Jean F.Brunel, *Microdendron* Jean F.Brunel, *Odontadenii* (Jean F.Brunel & Jacq.Roux) R.W.Bouman and *Praephyllanthus* Jean F.Brunel are here not retained as separate sections, otherwise this would render section *Moeroris* polyphyletic. Subgenus *Moeroris* comprises two clades (see Bouman *et al.* 2021; Supplementary fig. 1), that are both mixed with at least one of the other sections. To prevent polyphyly and because of the lack of morphological distinctness (mainly pollen characters) they are here subsumed. It is possible that some sections might be reinstated after a closer study of the two major clades in subgenus *Moeroris*.

4. Only two species of *Phyllanthus* subsection *Pentaphylli* of Webster (1956, 1958) have been included in a phylogenetic study (Falcón *et. al.* 2020), but as they show a general similarity with the species of genus *Moeroris*, they might prove to be nested within that genus. Further research is needed to test whether the other endemics in Hispaniola and Cuba to conform one or more groups with synapomorphies to define a natural infraclasification inside this subgenus.

Included species and taxonomic changes (179 spp.):

Moeroris airy-shawii (Brunel & Roux 1984: 470) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus airy-shawii* Jean F.Brunel & J.P.Roux.

Moeroris amnicola (Webster 1955: 54) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amnicola* G.L.Webster.

Moeroris ampandrandavae (Leandri 1957: 224) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ampandrandavae* Leandri.

Moeroris andranovatensis (Brunel & Roux 1981: 400) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus andranovatensis* Jean F.Brunel & J.P.Roux.

Moeroris angustata (Hutchinson *in* Fries 1914: 121) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus angustatus* Hutch.

Moeroris ankazobensis (Ralimanana & Hoffmann *in* Ralimanana *et al.* 2013: 542) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ankazobensis* Ralim. & Petra Hoffm.

Moeroris arvensis (Müller 1864: 332) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus arvensis* Müll.Arg.

Moeroris aspersa (Brunel & Roux 1985: 386) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aspersus* Jean F.Brunel & J.P.Roux.

Moeroris asperulata (Hutchinson 1920: 27) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus asperulatus* Hutch.

Moeroris austroparensis (Radcliffe-Smith 1992: 679) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus austroparensis* Radcl.-Sm.

Moeroris bancilhonae (Brunel & Roux 1980: 175) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bancilhonae* Jean F.Brunel & J.P.Roux.

Moeroris benguelensis (Müller 1864: 331) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus benguelensis* Müll.Arg.

Moeroris bequaertii (Robyns & Lawalrée 1947: 265) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bequaertii* Robyns & Lawalrée.

Moeroris boehmii (Pax 1893: 525) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus boehmii* Pax.

Moeroris bonnardii (Brunel 1987: 349) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bonnardii* Jean F.Brunel.

Moeroris borenensis (Gilbert 1987: 354) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus borenensis* M.G.Gilbert.

Moeroris brachyphylla (Urban 1914: 452) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus brachyphyllus* Urb.

Moeroris brynaertii (Brunel 1987: 351) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus brynaertii* Jean F.Brunel.

Moeroris buchii (Urban 1902: 288) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus buchii* Urb.

Moeroris burundiensis (Brunel 1987: 340) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus burundiensis* Jean F.Brunel.

Moeroris caesiifolia (Hoffmann & Cheek 2003: 439) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caesiifolius* Petra Hoffm. & Cheek.

Moeroris caespitosus (Brenan 1967: 258) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caespitosus* Brenan.

Moeroris caligata (Brunel & Roux 1985: 384) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caligatus* Jean F.Brunel & J.P.Roux.

Moeroris camerunensis (Brunel 1987: 353) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus camerunensis* Jean F.Brunel.

Moeroris caribaea (Urban 1908: 382) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caribaeus* Urb.

Moeroris carunculata (Brunel 1987: 380) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carunculatus* Jean F.Brunel, homotypic synonym: *Phyllanthus Phyllanthus pseudocarunculatus* Radcliffe-Smith (1996: 318), nom. illeg. superfl.

Moeroris ceratostemon (Brenan 1967: 259) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ceratostemon* Brenan.

Moeroris chevalieri (Beille 1908: 57) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chevalieri* Beille

Moeroris confusa (Brenan 1954: 68) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus confusus* Brenan.

Moeroris consanguinea (Müller 1866: 378) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus consanguineus* Müll.Arg.

Moeroris coursii (Leandri 1957: 226) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus coursii* Leandri.

Moeroris crassinervia (Radcliffe-Smith 1981: 766) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus crassinervius* Radcl.-Sm.

Moeroris debilis (Klein ex Willdenow 1805: 582) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus debilis* J.G.Klein ex Willd.

Moeroris dekindtiana (Brunel 1987: 352) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dekindtianus* Jean F.Brunel.

Moeroris delagoensis (Hutchinson 1920: 28) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus delagoensis* Hutch.

Moeroris denticulata (Brunel 1987: 365) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus denticulatus* Jean F.Brunel.

Moeroris dewildeorum (Gilbert 1987: 356) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dewildeorum* M.G.Gilbert.

Moeroris dictyophlebsis (Radcliffe-Smith 1992: 680) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dictyophlebsis* Radcl.-Sm.

Moeroris dimorpha (Britton & Wilson *in* Britton 1920: 75) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dimorphus* Britton & P.Wilson.

Moeroris dinteri (Pax 1909a: 75) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dinteri* Pax.

Moeroris discolaciniata (Brunel 1987: 349) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus discolaciniatus* Jean F.Brunel.

Moeroris dumetosa (Poiret 1804: 303) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dumetosus* Poir.

Moeroris dusenii (Hutchinson 1911: 314) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dusenii* Hutch.

Moeroris echinosperma (Wright 1870: 108) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus echinospermus* C.Wright.

Moeroris eliae (Brunel & Roux 1976: 375) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sublanatus* Schumach. & Thonn. subsp. *eliae* Jean F.Brunel & J.P.Roux, homotypic synonym: *Phyllanthus eliae* (Jean F.Brunel & J.P.Roux) Brunel (1987: 377).

Moeroris epiphylliferens (Brunel 1987: 347) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus epiphylliferens* Jean F.Brunel.

Moeroris fadyenii (Urban 1909: 13) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fadyenii* Urb.

Moeroris felicis (Brunel 1987: 385) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus felicis* Jean F.Brunel.

Moeroris fischeri (Pax 1894: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fischeri* Pax.

Moeroris fluminis-athi (Radcliffe-Smith 1974: 439) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fluminis-athi* Radcl.-Sm.

Moeroris fotii (Brunel 1987: 364) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fotii* Jean F.Brunel.

Moeroris friesii (Hutchinson 1914: 121) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus friesii* Hutch.

Moeroris fuertesii (Urban 1914: 451) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fuertesii* Urb.

Moeroris gabonensis (Brunel 1987: 350) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gabonensis* Jean F.Brunel.

Moeroris gagnioevae (Brunel & Roux 1980: 175) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gagnioevae* Jean F.Brunel & J.P.Roux.

Moeroris geniculatostemon (Brunel 1987: 364) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus geniculatostemon* Jean F.Brunel.

Moeroris gillettiana (Brunel 1987: 365) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gillettianus* Jean F.Brunel.

Moeroris gossweileri (Hutchinson 1911: 315) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gossweileri* Hutch.

Moeroris harrisii (Radcliffe-Smith 1981: 768) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus harrisii* Radcl.-Sm.

Moeroris heterophylla (Meyer ex Müller 1863: 43) R.W.Bouman, *comb. nov.* Based on: *Phyllanthus incurvus* Sonder (1850: 135), nom. illeg., non *Phyllanthus incurvus* Thunberg (1794: 24), heterotypic synonym: *Phyllanthus heterophyllus* E.Mey. ex Müll.Arg.

Moeroris hexadactyla (McVaugh 1961: 195) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hexadactylus* McVaugh.

Moeroris hildebrandtii (Pax 1893: 526) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hildebrandtii* Pax.

Moeroris holostylus (Milne-Redhead 1937: 414) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus holostylus* Milne-Redh.

Moeroris humpatana (Brunel 1987: 352) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus humpatanus* Jean F.Brunel.

Moeroris hutchinsoniana (Moore 1911: 192) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hutchinsonianus* S.Moore

Moeroris imbricata (Webster 1955: 56) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus imbricatus* G.L.Webster.

Moeroris irrigua (Radcliffe-Smith 1974: 440) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus irriguus* Radcl.-Sm.

Moeroris ivohibea (Leandri 1938: 197) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ivohibeus* Leandri.

Moeroris jaegeri (Brunel & Roux 1980: 176) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus jaegeri* Jean F.Brunel & J.P.Roux.

Moeroris juncea (Müller 1866: 411) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus junceus* Müll.Arg.

Moeroris kaessneri (Hutchinson 1911: 315) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kaessneri* Hutch.

Moeroris kelleana (Brunel 1987: 374) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kelleanus* Jean F.Brunel.

Moeroris kivuensis (Brunel 1987: 341) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kivuensis* Jean F.Brunel.

Moeroris lanceolata (Poiret 1804: 299) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lanceolatus* Poir.

Moeroris lebrunii (Robyns & Lawalrée 1947: 264) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lebrunii* Robyns & Lawalrée.

Moeroris leonardiana (Lisowski, Malaisse & Symoens 1974: 200) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leonardianus* Lisowski, Malaisse & Symoens.

Moeroris leptoneura (Urban 1912: 246) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leptoneurus* Urb.

Moeroris leptophylla (Müller 1866: 411) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leptophyllus* Müll.Arg.

Moeroris leschenaultii (Müller 1863: 37) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leschenaultii* Müll.Arg.

Moeroris letestui (Brunel 1987: 361) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus letestui* Jean F.Brunel.

Moeroris leucantha (Pax 1893: 524) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leucanthus* Pax.

Moeroris leucocalyx (Hutchinson 1911: 316) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leucocalyx* Hutch.

Moeroris leucochlamys (Radcliffe-Smith *in* Radcliffe-Smith & Hoffmann (2006: 610) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leucochlamys* Radcl.-Sm.

Moeroris leucosepala (Brunel 1987: 363) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leucosepalus* Jean F.Brunel.

Moeroris limmuensis (Cufodontis 1947: 484) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus limmuensis* Cufod.

Moeroris lindbergii (Müller 1873: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lindbergii* Müll.Arg.

Moeroris lokohensis (Leandri 1957: 229) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lokohensis* Leandri.

Moeroris lunifolia (Gilbert & Thulin 1993: 171) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lunifolius* Gilbert & Thulin.

Moeroris macrantha (Pax 1894: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus macranthus* Pax.

Moeroris madagascariensis (Müller 1863: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus madagascariensis* Müll.Arg.

Moeroris maestrensis (Urban 1924: 193) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus maestrensis* Urb.

Moeroris mafingensis (Radcliffe-Smith 1996: 308) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mafingensis* Radcl.-Sm.

Moeroris magdemeana (Brunel 1987: 362) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus magdemeanus* Jean F.Brunel.

Moeroris magnificens (Brunel & Roux 1981: 82) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus magnificens* Jean F.Brunel & J.P.Roux.

Moeroris mahengeaensis (Brunel 1987: 356) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mahengeaensis* Jean F.Brunel.

Moeroris makitae (Brunel 1987: 354) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus makitae* Jean F.Brunel.

Moeroris manniana (Müller 1864: 514) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mannianus* Müll.Arg.

Moeroris mckenziei (Fosberg 1978: 189) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mckenziei* Fosberg.

Moeroris melleri (Müller 1864: 514) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus melleri* Müll.Arg.

Moeroris meyeriana (Müller 1863: 42) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus meyerianus* Müll.Arg.

Moeroris micrantha (Richard 1850: 216) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus micranthus* A.Rich.

Moeroris microdendron (Welwitsch ex Müller 1864: 330) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus microdendron* Welw. ex Müll.Arg.

Moeroris micromeris (Radcliffe-Smith 1981: 769) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus micromeris* Radcl.-Sm.

Moeroris microphyllina (Müller 1864: 332) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus microphyllinus* Müll.Arg.

Moeroris microphylla (Kunth 1817: 87) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus microphyllus* Kunth.

Moeroris mieschii (Brunel & Roux 1981: 87) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mieschii* Jean F.Brunel & J.P.Roux.

Moeroris mindouliensis (Brunel 1987: 377) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mindouliensis* Jean F.Brunel.

Moeroris mitteniana (Hutchinson *in* Brown *et al.* 1912: 725) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mittenianus* Hutch.

Moeroris minutula (Müller 1873: 54) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus minutulus* Müll.Arg.

Moeroris mkurirae (Brunel 1987: 364) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mkurirae* Jean F.Brunel.

Moeroris moeroensis (De Wildeman 1906: 273) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus moeroensis* De Wild.

Moeroris monroviae (Brunel 1987: 346) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus monroviae* Jean F.Brunel.

Moeroris mooneyi (Gilbert 1987: 357) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mooneyi* M.G.Gilbert.

Moeroris moramangica (Leandri 1938: 197) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus melleri* Müll.Arg. subsp. *moramangicus* Leandri, homotypic synonym: *Phyllanthus moramangicus* (Leandri) Leandri (1958: 84).

Moeroris myrtacea (Sonder 1850: 134) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus myrtaceus* Sond.

Moeroris ndikinimekiana (Brunel 1987: 352) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ndikinimekianus* Jean F.Brunel.

Moeroris nigericus (Brenan 1950: 215) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nigericus* Brenan.

Moeroris niruroides (Müller 1864: 331) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus niruroides* Müll.Arg.

Moeroris nozeraniana (Brunel & Roux 1985: 382) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nozeranianus* Jean F.Brunel & J.P.Roux.

Moeroris nyale (Hoffmann & Cheek 2003: 442) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nyale* Petra Hoffm. & Cheek.

Moeroris nyikae (Radcliffe-Smith 1996: 317) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nyikae* Radcl.-Sm.

Moeroris oblongiglans (Gilbert 1987: 359) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus oblongiglans* M.G.Gilbert.

Moeroris odontadenioides (Brunel 1987: 342) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus odontadenioides* Jean F.Brunel.

Moeroris odontadenia (Müller 1864: 331) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus odontadenius* Müll.Arg.

Moeroris omahakensis (Dinter & Pax *in* Pax 1910: 234) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus omahakensis* Dinter & Pax.

Moeroris oppositifolia (Baillon ex Müller 1863: 24) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus oppositifolius* Baill. ex Müll.Arg.

Moeroris oxycoccifolia (Hutchinson 1912: 735) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus oxycoccifolius* Hutch.

Moeroris palakondensis (Raja Kullayiswamy & Sarojini in Raja Kullayiswamy et al. 2021: 2) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus palakondensis* Raja Kullayisw. & Sarojin.

Moeroris parva (Hutchinson 1911: 316) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus parvus* Hutch.

Moeroris paxii (Hutchinson 1911: 316) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus paxii* Hutch.

Moeroris pendula (Roxburgh 1832: 662) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pendulus* Roxb.

Moeroris pentaphylla (Wright ex Grisebach 1865: 167) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pentaphyllus* C.Wright ex Griseb.

Moeroris phillyreifolia (Poiret 1804: 299) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus phillyreifolius* Poir.

Moeroris pierlotii (Brunel 1987: 354) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pierlotii* Jean F.Brunel.

Moeroris pileostigma (Coode 1978: 119) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pileostigma* Coode.

Moeroris procera (Wright 1870: 149) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus procerus* C.Wright.

Moeroris prostrata (Müller 1864: 330) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus prostratus* Müll.Arg.

Moeroris pseudoniruri (Müller 1864: 539) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pseudoniruri* Müll.Arg.

Moeroris pulverulenta (Urban 1924: 192) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pulverulentus* Urb.

Moeroris pusilla (Brunel 1987: 400) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pusillus* Jean F.Brunel, heterotypic synonym: *Phyllanthus udoricola* Radcliffe-Smith (1996: 326).

Moeroris rangoloakensis (Leandri 1938: 198) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rangoloakensis* Leandri.

Moeroris raynalii (Brunel & Roux 1985: 387) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus raynalii* Jean F.Brunel & J.P.Roux.

Moeroris retinervis (Hutchinson *in* Brown *et al.* 1912: 735) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus retinervis* Hutch.

Moeroris rheedei (Wight 1852: t. 1895) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rheedei* Wight.

Moeroris rhizomatosa (Radcliffe-Smith 1982: 427) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rhizomatosus* Radcl.-Sm.

Moeroris rotundifolia (Klein ex Willdenow 1805: 584) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rotundifolius* J.G.Klein ex Willd.

Moeroris rouxii (Brunel 1980: 489) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rouxii* Jean F.Brunel.

Moeroris schaulsii (Brunel 1987: 399) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus schaulsii* Jean F.Brunel.

Moeroris selbyi (Britton & Wilson *in* Britton 1920: 74) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus selbyi* Britton & P.Wilson.

Moeroris sepialis (Müller 1880: 25) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sepialis* Müll.Arg.

Moeroris serandii (Brunel 1987: 353) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus serandii* Jean F.Brunel.

Moeroris shabaensis (Brunel 1987: 364) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus shabaensis* Jean F.Brunel.

Moeroris standleyi (McVaugh 1961: 199) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus standleyi* McVaugh, homotypic synonym: *Phyllanthus perpusillus* Standley (1948: 178), nom. superfl., *non Phyllanthus perpusillus* Baillon (1865: 358).

Moeroris stipulata Rafinesque (1838: 91), homotypic synonym: *Phyllanthus stipulatus* (Raf.) G.L.Webster (1955: 53).

Moeroris sublanata (Schumacher & Thonning 1827: 420) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sublanatus* Schumach. & Thonn.

Moeroris suffrutescens (Pax 1893: 523) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus suffrutescens* Pax.

Moeroris tanaensis (Brunel 1987: 361) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tanaensis* Jean F.Brunel.

Moeroris tanzaniana (Brunel 1987: 399) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tanzanianus* Jean F.Brunel.

Moeroris tayloriana (Brunel 1987: 355) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus taylorianus* Jean F.Brunel.

Moeroris tenuis (Radcliffe-Smith 1996: 323) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuis* Radcl.-Sm.

Moeroris thulinii (Radcliffe-Smith 1981: 774) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus thulinii* Radcl.-Sm.

Moeroris trichotepala (Brenan 1953: 91) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus trichotepalus* Brenan.

Moeroris tukuyuana (Brunel 1987: 356) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tukuyuanus* Jean F.Brunel.

Moeroris ukagurensis (Radcliffe-Smith 1981: 774) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ukagurensis* Radcl.-Sm.

Moeroris upembaensis (Brunel 1987: 367) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus upembaensis* Jean F.Brunel.

Moeroris vanderystii (Hutchinson & De Wildeman 1932: 470) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vanderystii* Hutch. & De Wild.

Moeroris vatovaviensis (Leandri ex Ralimanana & Hoffmann in Ralimanana *et al.* 2013: 551) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vatovaviensis* Leandri ex Ralim. & Petra Hoffm.

Moeroris venustula (Leandri 1938: 198) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus venustulus* Leandri.

Moeroris vichadensis (Croizat 1945: 181) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vichadensis* Croizat.

Moeroris virgulata (Müller 1864: 330) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus virgulatus* Müll.Arg.

Moeroris volkensii (Engler 1895: 236) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus volkensii* Engl.

Moeroris wingfieldii (Radcliffe-Smith 1981: 776) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus wingfieldii* Radcl.-Sm.

Moeroris wittei (Robyns & Lawalrée 1947: 266) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus wittei* Robyns & Lawalrée.

Moeroris xiphophora (Brunel 1987: 344) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus xiphophorus* Jean F.Brunel.

Moeroris xylorrhiza (Thulin 2005: 385) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus xylorrhizus* Thulin.

Moeroris yangambiensis (Brunel 1987: 336) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus yangambiensis* Jean F.Brunel.

Moeroris youngii (Brunel 1987: 335) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus youngii* Jean F.Brunel.

Moeroris zambica (Radcliffe-Smith 1996: 328) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus zambicus* Radcl.-Sm.

Moeroris zornioides (Radcliffe-Smith 1996: 328) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus zornioides* Radcl.-Sm.

Moeroris Raf. subgenus **Swartziani** (G.L.Webster) R.W.Bouman, comb. nov.

Phyllanthus L. subgenus *Swartziani* (G.L.Webster) Ralimanana & Hoffmann *in* Ralimanana *et al.* (2013: 536).—*Phyllanthus* subgenus *Phyllanthus* section *Phyllanthus* subsection *Swartziani* Webster (1955: 53); (1957: 306); (1970: 68); (2002a: 6); Brunel (1987: 345).—*Phyllanthus* L. section *Anthophyllus* Jean F.Brunel subsection *Swartziani* (G.L.Webster) Brunel (1987: 333).—Type: *Phyllanthus amarus* Schumach. & Thonn. = *Moeroris amara* (Schumach. & Thonn.) R.W.Bouman.

Reverchonia Gray (1880: 107); Pax & Hoffmann (1931: 66); Webster & Miller (1963: 200); Webster (1994: 45).—*Phyllanthus* L. section *Reverchonia* (A.Gray) Webster (2007: 235).—Type: *Reverchonia arenaria* A.Gray (= formerly *Phyllanthus warnockii* G.L.Webster) = *Moeroris arenaria* (A.Gray) R.W.Bouman.

Diagnostic features: Herbs, monoecious, branching phyllanthoid with pinnatiform branchlets or non-phyllanthoid branching (spiral phyllotaxy). *Brachyblasts* absent. *Leaves* distichous or spiral. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals (4)5 or 6; disc glands 5 or 6, free or entire and around base of stamens (H-shaped) in *M. arenaria*; stamens (2 or) 3, filaments entirely or partially connate; anthers dehiscing obliquely or horizontally (vertically in *M. arenaria*); pollen 3-colporate, exine reticulate. *Pistillate flowers*: sepals 6; disc entire; ovary 3-locular, smooth or slightly rugose; style absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or finely striated longitudinally.

Distribution: Africa and North America with some common invasive species.

Note—This group contains an enigmatic species (*M. arenaria*) originially placed in the separate genus *Reverchonia* A.Gray. This species differs in most major characters (staminate flower and branching type) from all others in the subgenus, but retaining it in a separate section, would result in a paraphyletic group.

Included species and taxonomic changes (4 spp.):

Moeroris abnormis (Baillon 1860: 42) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus abnormis* Baill.

Moeroris amara (Schumacher & Thonning 1827: 421) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amarus* Schumach. & Thonn.

Moeroris arenaria (Gray 1880: 107) R.W.Bouman, *comb. nov.* Basionym: *Reverchonia arenaria* A.Gray (non *Phyllanthus arenarius* Beille 1927: 587), homotypic synonym: *Phyllanthus warnockii* Webster (2007: 235).

Moeroris fraterna (Webster 1955: 53) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fraternus* G.L.Webster.

Moeroris Raf. subgenus **Tenellanthus** (Jean F.Brunel) R.W.Bouman, comb. nov.

Phyllanthus L. subgenus *Tenellanthus* Brunel (1987: 301); Ralimanana & Hoffmann (2011: 358).—Type: *Phyllanthus tenellus* Roxb. = *Moeroris tenella* (Roxb.) R.W.Bouman.

Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Pentandra* Webster (1967b: 333); (1970: 63); (1997: 218); (2001b: 385).—*Phyllanthus* L. subgenus *Tenellanthus* Jean F.Brunel section *Pentandra* (G.L.Webster) Brunel (1987: 313); Schmid (1991: 63).—Type: *Phyllanthus pentandrus* Schumach. & Thonn. = *Moeroris pentandra* (Schumach. & Thonn.) R.W.Bouman.

Phyllanthus L. subgenus *Tenellanthus* Jean F.Brunel section *Loandani* Brunel (1987: 309).—Type: *Phyllanthus loandensis* Welw. = *Moeroris loandensis* (Welw.) R.W.Bouman.

Diagnostic features: Herbs or (sub)shrubs, monoecious, branching (sub)phyllanthoid, branchlets (bi)pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5; stamens (3 in *M. cocumbiensis* (Jean F.Brunel) R.W.Bouman) 5(–7 in *M. nummulariifolius* (Müll.Arg.) R.W.Bouman), filaments free, anthers basifixed, dehiscing longitudinally; pollen subglobose, 3- or 4-colporate, exine reticulate. *Pistillate flowers*: sepals 5, obovate or orbicular; disc entire, shallowly cupuliform; ovary 3-locular, smooth or slightly rugose; style absent or short; stigmas bifid. *Fruits* capsules, style persistent or caducous. *Seeds* trigonous, papillose or verrucose.

Distribution: Mainly Africa with one common invasive (*M. tenellus* (Roxb.) R.W.Bouman).

Notes—1. Previously placed in subgenus *Kirganelia* on the basis of the 5-merous staminate flowers (Webster 1967), but later separated by Brunel (1987), a conclusion upheld by Ralimanana & Hoffmann (2011). Most of the species in this group are small herbs or subshrubs with *M. tenellus* being invasive in all tropics and parts of some temperate regions.

2. The three sections recognized by Brunel (1987) are mainly based on differences in pollen morphology and are morphologically difficult to identify, which is why they are synonymized here under subgenus *Tenellanthus*.

Included species and taxonomic changes (16 spp.):

Moeroris ajmeriana (Chaudhary & Rao 2002: 147) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ajmerianus* L.B.Chaudhary & R.R.Rao.

Moeroris angolensis (Müller 1864: 329) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus angolensis* Müll.Arg.

Moeroris cocumbiensis (Brunel 1987: 315) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cocumbiensis* Jean F.Brunel.

Moeroris comorensis (Leandri 1938: 194) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus comorensis* Leandri.

Moeroris frazieri (Radcliffe-Smith 1982: 425) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus frazieri* Radcl.-Sm.

Moeroris graminicola (Hutchinson 1911: 191) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus graminicola* Hutch.

Moeroris hodjelensis (Schweinfurth 1899: 304) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hodjelensis* Schweinf.

Moeroris loandensis (Welwitsch ex Müller 1864: 329) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus loandensis* Welw. ex Müll.Arg.

Moeroris manicaensis (Brunel ex Radcliffe-Smith 1996: 309) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus manicaensis* Jean F.Brunel ex Radcl.-Sm.

Moeroris martinii (Radcliffe-Smith 1996: 311) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus martinii* Radcl.-Sm.

Moeroris mendesii (Brunel 1987: 314) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mendesii* Jean F.Brunel.

Moeroris nummulariifolia (Poiret 1804: 302) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nummulariifolius* Poir.

Moeroris parvula (Sonder 1850: 132) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus parvulus* Sond.

Moeroris pentandra (Schumacher & Thonning 1827: 419) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pentandrus* Schumach. & Thonn.

Moeroris tenella (Roxburgh 1832: 668) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenellus* Roxb.

Moeroris tsetserrae (Brunel 1987: 310) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tsetserrae* Jean F. Brunel.

Clade E—Figs. 1, 2G & H (supplementary fig. 1)

Phyllanthus L.

Phyllanthus Linnaeus (1753: 981); de Jussieu (1824: 21); Gaertner (1790: 125); Baillon (1858: 621); Müller (1866: 274); Hooker (1887: 285); Webster (1994: 44); (1997: 206); Radcliffe-Smith (2001: 38); Webster (2014: 78); Chakrabarty & Balakrishnan (2018: 258).—*Phyllanthus* L. section *Euphyllanthus* Grisebach (1859: 33), nom. inval.; Baillon (1860: 24); (1862b: 237); (1865: 351); Müller (1863: 3); (1866: 374).—Lectotype (designated by Small 1913): *Phyllanthus niruri* L.

Diagnostic features: Herbs, shrubs to trees, monoecious or dioecious, branching (non-)phyllanthoid, rarely rooting at nodes with main stem transformed to rootstock (*Phyllanthus* section *Callitrichoides*), branchlets (bi)pinnatiform, sometimes transformed into phylloclades, stems rarely ornamented with small platelets. *Brachyblasts* absent (or present in section *Omphacodes*). *Cataphyllary stipules* triangular to elongate to squamiform to linear-elliptic to slightly spinescent, indurate or membranous, sometimes fused with cataphylls, base (bilaterally) auriculate or not. *Cataphylls* triangular or oblong-elliptic to linear, indurate or membranous, usually darker colored (laminate in *P. formosus* Urb.), sometimes only on orthotropic branches, then branchlets sometimes subtended by slightly smaller leaves instead of cataphylls. *Leaves* usually distichous and alternate (opposed in *Phyllanthus* section *Williamia* (Baill.) Müll.Arg. subsection *Mirifici* G.L.Webster) to spiral, or reduced to scales similar to cataphylls. *Inflorescences* axillary (to rami- and cauliflorous), unisexual or bisexual fascicles, sometimes paniculate (spiciform thyrses or racemes in *P. almadensis* Müll.Arg.). *Staminate flowers*: sepals 4–8; disc entire, 3–6 free to slightly united glands or 3 duplex glands; stamens 2–7(–15 in *Phyllanthus* section *Williamia*), filaments free to (basally) connate, or arranged in whorls with varied degree of fusion, anthers usually ovoid, dehiscing horizontally to vertically, connectives (non-)apiculate, sometimes all parts completely connate into a synandrium; pollen (sub)prolate to spheroidal, 3- or 4(–11)-colporate, clypeate, (diplo)porate without distinct ectocolpi, pantoporate with elongated colpi or colpi anastomosing around exine shields, colpi monoporate when present, exine semitectate-reticulate, vermiculate or pilate; pistillode absent. *Pistillate flowers*: sepals 4–10; disc entire, sometimes cupuliform or consisting of free glands; ovary 3- or 4(–6)-locular; style present or absent; stigmas free or connate, with bifid to multifid or entire tips, sometimes lacerate, reduced to petaloid structures or fused into a calyptra on top of the ovary. *Fruits* capsules (sometimes massive) or baccate. *Seeds* trigonous or globose, with or without sarcotesta, smooth, obscurely striate, puncticulate, rugulose, finely reticulate, ribbed or verrucate.

Distribution: Mainly Americas and West Indies, some invasive species.

Notes—1. The genus *Phyllanthus* is here drastically reduced in size: it now comprises fewer than 200 species and it is mainly distributed in the Americas. Morphological variation within the genus remains extensive, with some overlap with other genera. This is a direct consequence of widespread morphological convergence in the tribe *Phyllantheae* and is the main cause of many of the taxonomic problems that have plagued this group. There is not a set of characters unique to *Phyllanthus* as there are always some exceptions. Geographically, species in the genus *Phyllanthus* are restricted mostly to the Americas, aside from some invasive species like *P. niruri*. Genera previously classified in a broader treatment of *Phyllanthus* that are also found in South America are *Moeroris* and a few species of *Cicca*. *Phyllanthus* in its current circumscription can be distinguished from other genera in tribe Phyllantheae mainly by comparing specifically similar sections or subgenera. For example, *Phyllanthus* section *Loxopodium* is very similar to *Cathetus* subgenus *Macraea* and these groups are mainly distinguished by their pollen and some vegetative characters, but they are geographically separated. *Nymphanthus* is easily distinguished from *Phyllanthus* on the basis

of its tetramerous flowers; these also occur in *Phyllanthus* section *Glyptothamnus* G.L.Webster, but the staminate flowers in the latter have an entire disc (versus free glands in *Nymphanthus*). Some species of *Phyllanthus* subgenus *Conami* (Aubl.) G.L.Webster or *Microglochidion* Müll.Arg. can resemble those in *Cicca* subgenus *Gomphidium*, differing mainly in their pollen, staminate flowers (filaments fused or not) or pistillate flowers (shape of the styles and stigmas).

2. For some species listed below we could not determine their subgeneric alignment due to the unavailability of specimens, unresolved phylogenetic relationships or incomplete descriptions. Webster in one of his unpublished manuscripts (2002 outline of the Neotropical *Phyllanthus*), discussed the affinity of *P. orinocensis* Steyerm. (Steyermark *et al.* 1952: 321) and *P. bolivarensis* Steyerm. (Steyermark *et al.* 1952: 317) and considered them to be better placed in the genus *Sebastiania* Spreng. (Euphorbiaceae), but this has not yet been confirmed.

3. Section *Ciccopsis* is retained in *Phyllanthus*, but placement in any specifc subgenus awaits further phylogenetic studies to resolve its full affinities. Falcón *et al.* (2020) recovered *P. pseudocicca* Grisebach (1865: 166) in a large Neotropical clade with weak support as close to subgenus *Conami*.

Included, but further unplaced species (9 spp.): *P. bolivarensis* Steyerm., *P. harrimanii* Webster (1978: 570), *P. hortensis* Govaerts & Radcliffe-Smith (1996: 177), *P. lasiogynus* Müller (1866: 357), *P. orinocensis* Steyerm., *P. petaloideus* Wilson (1962: t. 3589), *P. pseudoguyanensis* Herter & Mansfeld (1936 publ. 1937: 33), *P. pulcherrimus* Herter ex Arechavaleta (1925: 72), *P. sellowianus* (Klotzsch 1841: 200) Müller (1863: 37).

Phyllanthus L. (subgenus *incertae sedis*) section **Ciccopsis** G.L.Webster

Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Ciccopsis* Webster (1955: 57); (1957: 61).—Type: *Phyllanthus pseudocicca* Griseb.

Diagnostic features: Shrubs or trees, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, on separate branchlets; either only proximal staminate inflorescences subtended by cataphylls and distal bisexual inflorescences associated with normally developing leaves. *Staminate flowers*: sepals 6, reflexed; disc glands 6; stamens 3, filaments free, sometimes fused at base, anthers ovoid, dehiscing horizontally; pollen grains 3-colporate, aperture angular, exine reticulate. *Pistillate flowers:* sepals 6; disc entire, 3-angled; ovary 3-locular; styles absent; stigmas bifid. *Fruits* capsules with fleshy exocarp. *Seeds* trigonous, minutely verrucate along longitudinal lines.

Distribution: West Indies (Cuba).

Note—Webster (1957) did not include a description of the fruits and seeds of this monotypic section and its affinities remain unclear, but recent collections indicate that the fruits are capsular with 6 similar trigonous verrucate seeds (Falcón & Leyva 2020). Webster (1957) discussed the affinities of this species with section *Cicca*, but also with his *Phyllanthus* subgenus *Kirganelia* and possibly *Phyllanthus* subgenus *Xylophylla* section *Omphacodes*. Falcón *et al.* (2020) found it related to other Neotropical species of *Phyllanthus*, but its exact relation to extant subgenera is not resolved (supplementary fig. 1).

Included species (1 sp.): *Phyllanthus pseudocicca* Grisebach (1865: 166).

Phyllanthus L. (subgenus *incertae sedis*) section **Omphacodes** G.L.Webster

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Omphacodes* Webster (1955: 59); (1958: 142).—Type: *Phyllanthus subcarnosus* C.Wright ex Griseb.

Diagnostic features: Trees, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5, free or slightly united; stamens 3 (or 4), filaments connate, anthers muticous, dehiscing obliquely; pollen clypeate, exine shields polybrochate, reticulate. *Pistillate flowers*: sepals 5; disc shallowly cupuliform, tenuous (thin), margin undulate (wavy), not pitted; ovary 3-locular; style absent; stigmas bifid, branches rather thick. *Fruits* massive, indehiscent capsules, outer layer somewhat fleshy. *Seeds* trigonous, pairs often unequal, obscurely striate.

Distribution: West Indies.

Note—Falcón *et al.* (2020) found that *P. subcarnosus* was not a part of *Phyllanthus* subgenus *Xylophylla*, which is also confirmed here (supplementary fig. 1). More information is necessary to resolve its relationship within *Phyllanthus*.

Included species (1 sp.): *P. subcarnosus* Wright ex Grisebach (1865: 168).

Phyllanthus L. subgenus **Ciccastrum** (Müll.Arg.) R.W.Bouman, stat. nov.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Ciccastrum* Müller (1873: 26).—*Glochidion* J.R.Forst. & G. Forst. section *Ciccastrum* (Müll.Arg.) Pax & Hoffmann (1931: 58).—Type: *Phyllanthus riedelianus* Müll.Arg.

Diagnostic features: Shrubs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* unisexual or bisexual fascicles, forming a cauliflorous panicle in *P. riedelianus*. *Staminate flowers*: sepals 6, (highly unequal) biseriate; disc glands 6; stamens 3, filaments connate; anthers apiculate, dehiscing vertically; pollen spheroidal, clypeate, exine reticulate. *Pistillate flowers*: sepals 6; disc shallowly cupuliform; ovary 3-locular; style absent; stigmas entire, bifid or apically emarginate. *Fruits* capsules. *Seeds* rugulose, no further details known.

Distribution: Tropical South and Central America.

Included species (2 spp.): *P. purpusii* Brandegee (1914: 55), *P. riedelianus* Müller (1863: 16).

Phyllanthus L. subgenus **Conami** (Aubl.) G.L.Webster

Phyllanthus L. subgenus *Conami* (Aubl.) Webster (1956: 345); (1957: 363).—*Conami* Aublet (1775: 926, t. 354).—Type: *Conami brasiliensis* Aubl. (= *Phyllanthus brasiliensis* (Aubl.) Poir.)

Diagnostic features: Herbs, shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets (bi)pinnatiform (sometimes single or paired). *Brachyblasts* absent. *Cataphyllary stipules* triangular to elongate, indurate or membranous, base (not) auriculate. *Cataphylls* triangular or oblong-elliptic (only on orthotropic branches), but branchlets sometimes subtended by slightly smaller leaves instead of cataphylls. *Leaves* distichous. *Inflorescences* axillary, usually bisexual fascicles. *Staminate flowers*: sepals 6, in two (sometimes distinct) whorls, margins entire; disc entire or 3 duplex or 6 glands; stamens 3, filaments free or connate, anthers dehiscing ± horizontally, connectives non-apiculate; pollen spheroidal, 3-colporate with colpi diploporate or porate, exine vermiculate to pilate. *Pistillate flowers*: sepals 6, in two (sometimes distinct) whorls; disc cupular (segmented in *Phyllanthus* subgenus *Conami* section *Apolepsis*); ovary 3–6-locular, smooth; style absent; stigmas bifid. *Fruits* capsular. *Seeds* smooth or verrucate.

Distribution: Tropical South America.

Phyllanthus L. subgenus **Conami** (Aubl.) G.L.Webster section **Apolepis** G.L.Webster

Phyllanthus L. subgenus *Conami* (Aubl.) G.L.Webster section *Apolepis* Webster (1957: 371).—Type: *Phyllanthus orbiculatus* Rich.

Diagnostic features: Herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphylls* oblong-ellipic, membranous. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 6, whorls indistinct; disc glands 6; stamens 3, filaments free; anthers emarginate, dehiscing horizontally; pollen grains spheroidal, pantoporate, exine pilate. *Pistillate flowers*: sepals 6, one type; disc 6 segments; ovary 3-locular; style short; stigmas appressed to the ovary, bifid to halfway, tips incurved. *Fruits* capsules, veins indistict. *Seeds* trigonous, verrucate.

Distribution: Tropical South America.

Note—A monotypic section that differs significantly in habit and staminate floral morphology from *Phyllanthus* subgenus *Conami* section *Conami*. Webster (1957) placed this species in *Phyllanthus* subgenus *Conami* on the basis of the pilate exine, but this character was shown to have evolved several times (Meewis & Punt 1983; Bouman *et al.* 2021).

Included species (1 sp.): *Phyllanthus orbiculatus* Richard (1792: 113).

Phyllanthus subgenus **Conami** section **Calodictyon (**G.L.Webster) R.W.Bouman

Phyllanthus subgenus *Gomphidium* section *Calodictyon* Webster (1967a: 194).—Type: *Phyllanthus tuerckheimii* G.L.Webster.

Diagnostic features: Shrubs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphylls* probably present, but not seen or described. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers:* sepals 5, whorls indistinct; disc 3 duplex glands; stamens 3, filaments free; anthers muticous, anther slits longitudinal, dehiscing vertically; pollen 3-colporate or syncolporate, exine coarsely reticulate. *Pistillate flowers*: sepals 5; disc 5-angled, entire; ovary 3-locular; style present; stigma tips bifid. *Fruits* and seeds unknown.

Distribution: Central America: Guatemala and Mexico (Chiapas).

Note—Webster (1967a) described this species and placed it in a new section within *Phyllanthus* subgenus *Gomphidium* (Baill.) G.L.Webster. However, it is sister to subgenus *Conami* section *Conami* (supplementary fig. 1) and is here transferred. Free stamens occur in all subgenera of *Phyllanthus* and could perhaps be plesiomorphic.

Included species (1 sp.): *Phyllanthus tuerckheimii* Webster (1967a: 195).

Phyllanthus L. subgenus **Conami** (Aubl.) G.L.Webster section **Conami**

Phyllanthus L. subgenus *Conami* (Aubl.) G.L.Webster section *Conami*: Literature and type as under the subgenus.

Phyllanthus L. subgenus *Conami* (Aubl.) G.L.Webster section *Nothoclema* Webster (1955: 56); (1957: 363); (2003: 21).—Type: *Phyllanthus acuminatus* Vahl.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets bipinnatiform. *Brachyblasts* absent. *Cataphylls* triangular, indurate. *Leaves* distichous, laminate leaves present on ultimate and penultimate axes. *Inflorescences* axillary, bisexual fascicles, usually on lateral (ultimate branches), sometimes on main axes. *Staminate flowers*: sepals 6, in two whorls; disc entire to dissected, usually 3 duplex glands; stamens 3, filaments connate, anthers dehiscing horizontally, connective sometimes elongated; pollen 3-colporate, colpi diploporate, or pantoporate with elongated colpi, exine varying from reticulate to vermiculate and pilate. *Pistillate flowers*: sepals 6, in two whorls; disc usually cupular; ovary 3-locular; style absent or short; stigmas erect or spreading, slender or dilated, bifid to lacerate. *Fruits* capsules, conspicuously veined. *Seeds* trigonous, sometimes asymmetric, smooth or puncticulate.

Distribution: Tropical South America and West Indies.

Note—The same nomenclatural issue as in *Kirganelia* is raised here as Webster (1955) created section *Nothoclema* as the type section for subgenus *Conami*. He later rectified this (Webster 1960), but did not follow it accordingly in subsequent papers (e.g., Webster 2003). The autonym name for this section, *Conami*, is applied here.

Included species (10 spp.): *P. acuminatus* Vahl (1791: 95), *P. anisolobus* Müller (1866: 382), *P. brasiliensis* (Aublet 1775: 926) Poiret (1804: 296), *P. caymanensis* Webster & Proctor (1984: 121), *P. graveolens* Kunth (1817: 112), *P. liesneri* Webster (2003: 26), *P. mcvaughii* Webster (1966: 339), *P. meridensis* Webster (2003: 27), *P. mocinoanus* Baillon (1860: 35), *P. pavonianus* Baillon (1860: 30).

Phyllanthus L. subgenus **Microglochidion** (Müll.Arg.) Jean F.Brunel

Phyllanthus L. subgenus *Microglochidion* (Müll.Arg.) Brunel (1987: 237).—*Glochidion* J.R.Forst. & G.Forst. section *Microglochidion* Müller (1863: 58, 69); Pax & Hoffmann (1931: 58).—*Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz section *Microglochidion* (Müll.Arg.) Müller (1865a: 370); (1866: 322); Jablonski (1967: 89).—Lectotype (designated by Jablonski 1967): *Glochidion vacciniifolium* Müll.Arg. (= *Phyllanthus vacciniifolius* (Müll.Arg.) Müll.Arg.)

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Francavillani* Brunel (1987: 236).—Type: *Phyllanthus francavillanus* Beille (= *Phyllanthus myrsinites* Kunth subsp. *francavillanus* (Mül.Arg.) G.L.Webster)

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* distichous, often with laminal glands. *Inflorescences* axillary, unisexual fascicles (or flowers (sub) solitary). *Staminate flowers*: sepals 6; disc

glands 3 (then opposite to stamens) or 6; stamens 3, filaments completely free or basally connate, anthers elongate, dehiscing extrorse, vertical, connectives apiculate; pollen (sub)prolate to subspheroidal, 4–11- colporate, colpi mono- or triporate, exine semitectate-reticulate. *Pistillate flowers*: sepals 6; disc entire; ovary 3-locular; styles present; stigmas entire or bifid. *Fruits* capsules. *Seeds* trigonous, unknown.

Distribution: Tropical South America.

Notes—1. We agree with Brunel's (1987) decision to raise this group to subgeneric level since it is distinct from other subgenera within *Phyllanthus*. This seems to be the best solution for the otherwise polyphyletic genus *Emblica*. The relation with subgenus *Xylophylla* has been discussed in Bouman *et al.* (2021), and merits further study, particularly the relation between colporate and clypeate pollen.

2. Part of *Phyllanthus* subgenus *Microglochidion* has been treated by Brunel (1987) as the *Adianthoides* group and *Francavillanus* group (following Jablonski 1967) within *Phyllanthus* subgenus *Xylophylla*. However, some of these species were subsequently treated by Webster (1999) as synonyms of *P. myrsinites* Kunth. (e.g., *P. adenophyllus* Müll. Arg., *P. dinizii* Huber, *P. francavillanus* Müll.Arg., *P. gallinetae* Jabl. and *P. pimichinianus* Jabl.) and the *Adianthoides* group as envisioned by Jablonski (1967) has been divided, whereby many species were transferred to other sections (see *Phyllanthus* subgenus *Xylophylla* section *Adianthoides* Jabl. ex Jean F.Brunel).

3. A full review of this group has not been undertaken since Müller (1866). Jablonski (1967) attempted this in a work on the *Phyllanthus* species from the Guayana Highlands, but did not provide a synopsis of this section. He mentioned that for many species the material was incomplete and required additional collections. Several species currently included in this section have no gland in the leaf lamina and the variation in stamens and styles is quite apparent. More collections and a denser phylogenetic sampling may show that some of the species are part of other sections in *Phyllanthus* subgenus *Xylophylla*. The inclusion here of section *Francavillani* might have to be reversed in the future. Both groups agree in general floral morphology, although Brunel (1987) did describe the pollen of section *Francavillani* Jabl. ex Jean F.Brunel as clypeate, which is more typical for *Phyllanthus* subgenus *Xylophylla*.

Included species (23 spp.): *P. aracaensis* Webster ex Secco & de Rosário (2015: 209), *P. carrenoi* Steyermark in Steyermark & Brewer-Carias (1976: 343), *P. chimantae* Jablonski (1967: 100), *P. duidae* Gleason (1931: 382), *P. huberi* Riina & Berry in Grande *et al.* (2012: 10), *P. jablonskianus* Steyermark & Luteyn (1984: 317), *P. jauaensis* Jablonski (1972: 865), *P. lediformis* Jablonski (1967: 103), *P. longistylus* Jablonski (1967: 100), *P. maguirei* Jablonski (1967: 105), *P. majus* Steyermark in Steyermark *et al.* (1952: 318), *P. minutifolius* Jablonski (1967: 115), *P. myrsinites* Kunth (1817: 111), *P. neblinae* Jablonski (1967: 107), *P. obfalcatus* Lasser & Maguire (1950: 79), *P. paraqueensis* Jablonski (1967: 104), *P. pycnophyllus* Müller (1866: 322), *P. strobilaceus* Jablonski (1967: 96), *P. subapicalis* Jablonski (1967: 101), *P. tepuicola* Steyermark (1975 publ. 1976: 236), *P. vacciniifolius* (Müller 1863: 69) Müller (1866: 322), *P. ventuarii* Jablonski (1967: 104), *P. websterianus* Steyermark (1958: 17).

Phyllanthus L. subgenus **Phyllanthus**

Phyllanthus L. subgenus *Phyllanthus*: Webster (1957: 170); (1970: 64); Brunel (1987: 329).—Type: *Phyllanthus niruri* L.
Niruri Adanson (1763: 356).—Lectotype (selected by Webster 1994): *Phyllanthus niruri* L.

Diagnostic features: Herbs or small shrubs, rarely aquatic, monoecious or dioecious, branching (sub-)phyllanthoid or non-phyllanthoid, branchlets pinnatiform or transformed to phylloclades. *Brachyblasts* absent. *Cataphyllary stipules* linear-elliptic, usually membranous, base (not) auriculate. *Cataphylls* when present, triangular to elliptic or ovate, sometimes leaves on main axes not reduced to cataphylls. *Leaves* when present alternate or subopposite, distichous, sometimes fleshy. *Inflorescences* axillary, unisexual or bisexual fascicles (spiciform thyrses or racemes at end of branchlets in *P. almadensis*). *Staminate flowers*: sepals 4–6; disc glands 4–6; stamens 2 or 3, filaments connate or free, anthers globular to elongate, sometimes stipitate, dehiscing vertically to horizontally, connectives non-apiculate; pollen 3- or 4-colporate, colpi monoporate, exine semitectate-reticulate. *Pistillate flowers*: sepals 5 or 6; disc usually entire, lobed or appearing as free glands; ovary 3-locular; style absent or short; stigmas bifid, sometimes capitate. *Fruits* capsules. *Seeds* trigonous, striate, ribbed or verrucate.

Distribution: Tropical South and Central America, with a pantropical invasive (*P. niruri*).

Note—Subgenus *Phyllanthus* as here circumscribed is Neotropical and includes several sections that exhibit a wide range of morphological characters. Other herbaceous species with phyllanthoid branching formerly placed in the genus *Phyllanthus* are now in the genera *Moeroris* (formerly *Phyllanthus* subgenus *Afroswartziani*, from Africa), *Emblica* (*E. urinaria* complex from Asia) or *Lysiandra* (from Australia). Some herbaceous sections with non-

phyllanthoid branching are included (e.g., section *Loxopodium* G.L.Webster (including *Salviniopsis* Jean F.Brunel), and *Antipodanthus* G.L.Webster).

Included species (section incertae sedis, 8 spp.): *P. bicolor* de Visiani (1858: 139), *P. cassioides* Rusby (1912: 100), *P. compressus* Kunth (1817: 109), *P. leptocaulos* Müller. (1873: 47), *P. paraguayensis* Parodi (1881: 50), *P. pohlianus* Müller (1873: 49), *P. simplicicaulis* Müller (1863: 38), *P. subcuneatus* Greenman (1898: 478).

Phyllanthus L. subgenus **Phyllanthus** section **Antipodanthus** (G.L.Webster) R.W.Bouman

Phyllanthus L. subgenus *Isocladus* section *Antipodanthus* Webster (2002b: 290).—Type: *Phyllanthus dictyospermus* Müll.Arg.

Diagnostic features: Subshrubs or shrubs, mostly dioecious (except *P. dawsonii* Steyerm.), branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* spiral, petiolate. *Inflorescences* axillary, unisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 3, filaments connate (or free in *P. rosmarinifolius*); anthers orbicular, dehiscing vertically to horizontally; pollen 3- or 4-colporate, colpi monoporate, exine coarsely reticulate. *Pistillate flowers*: sepals 6; disc shallowly cupuliform; ovary 3-locular; style absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or verrucate.

Distribution: Tropical South America.

Note—Originally placed within *Phyllanthus* subgenus *Isocladus* by Webster (2002b), but the group was shown to be nested within *Phyllanthus* subgenus *Phyllanthus* (Bouman *et al.* 2021) and is accordingly transferred. Webster (1966, 2002b) confused some species of *Phyllanthus* subgenus *Lysiandra* with *Phyllanthus* subgenus *Antipodanthus*, leading to some confusion in the study by Kathriarachchi *et al.* (2006), who included only one species of *Lysiandra* (then Australian *Phyllanthus* section *Antipodanthus*).

Included species (6 spp.): *P. dawsonii* Steyermark (1958: 13), *P. dictyospermus* Müller (1866: 394), *P. pinifolius* Baillon (1865: 353), *P. ramillosus* Müller (1863: 36), *P. rosmarinifolius* Müller (1873: 60), *P. salesiae* Silva (2009: 231).

Phyllanthus L. subgenus **Phyllanthus** section **Choretropsis** Müll.Arg.

Phyllanthus L. subgenus *Phyllanthus* section *Choretropsis* Müller. (1863: 4, 52); Müller (1866: 427); Baillon (1865: 359); Pax & Hoffmann (1931: 65); Santiago *et al.* (2006: 138).—Type: *Phyllanthus choretroides* Müll.Arg.

Phyllanthus section *Xylophylla* auct. non (L.) Baill.: Baillon (1858: 623), pro parte, without type.

Diagnostic features: Erect (sub)shrubs, monoecious, branching phyllanthoid or less frequently not distinguishable when all axes terete; main axes terete, subterete, succompressed or flattened, smooth or striate, glabrous; branched from the base, rarely branches restricted to the upper part of the plant; plagiotropic branchlets often terete or transformed to phylloclades, phylloclades cylindrical or flattened. *Brachyblasts* absent. *Cataphyllary stipules* triangular, base indurate, auriculate. *Cataphylls* squamiform. *Leaves* reduced to scales on plagiotropic branchlets, similar to the cataphylls. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 2 or 3, rarely 4, filaments free or connate, anthers, dehiscing longitudinally, horizontally or rarely obliquely; pollen 3–5-colporate, exine reticulate. *Pistillate flowers*: sepals 5 or 6; disc shallowly cupuliform; ovary 3-locular, depressed-globose; style present or absent; stigmas bifid to multifid. *Fruits* capsules. *Seeds* trigonous, verrucose or finely reticulate.

Distribution: Tropical South America.

Note—This South American section was often treated together with the West Indian *Phyllanthus* section *Xylophylla* (see Baillon 1865) on account of the reduced leaves and the presence of phylloclades in both sections. However, on closer examination of the flowers, architecture and pollen of the South American species, they were found to differ considerably and Webster (1957) already recommended to separate the South American species to *Phyllanthus* section *Choretropsis* Müll.Arg., which was later formally done by Santiago (1988). For a more extensive study of the whole section and its subsections, see Santiago *et al.* (2006).

Phyllanthus L. subgenus **Phyllanthus** section **Choretropsis** Müll.Arg. subsection **Applanata** L.J.M.Santiago

Phyllanthus L. subgenus *Phyllanthus* section *Choretropsis* Müll.Arg. subsection *Applanata* Santiago (1988: 45).—Type: *Phyllanthus klotzschianus* Müll.Arg.

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid; main axes terete; primary branchlets pinnatiform and modified into flattened phylloclades, sometimes bipinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular. *Cataphylls* ovate or elliptic, apex acute. *Leaves* reduced or not. *Inflorescences* axillary, usually bisexual, sometimes unisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 3, rarely 4, filaments free or connate, anthers globose, dehiscing longitudinally, horizontally or rarely obliquely. *Pistillate flowers*: sepals 5 or 6; disc entire; ovary 3-locular; stigmas thick, thin or filiform, rarely flattened, bifid or multifid. *Fruits* capsules, depressed globose or trigonous. *Seeds* trigonous, verrucose or finely reticulate.

Distribution: Tropical South America.

Note—One new name is proposed here for *P. scoparius* Müller (1873:74), because the epithet is illegitimate due to the synonimized name *P. scoparius* Welwitsch (1859: 591). We propose the name *P. saxatilis* Strijk & R.W.Bouman due to the plant occurring mostly on rocky soils (Santiago *et al.* 2006).

Included species (8 spp.): *P. angustissimus Müller (1863: 55), P. dracaenoides* Orlandini & Cordeiro (in Orlandini *et al.* 2021: 1011), *P. edmundoi Santiago* (1988: 46), *P. flagelliformis* Müller (1863: 54), *P. gladiatus* Müller (1863: 52), *P. klotzschianus* Müller (1863: 53), *P. pedicellatus* Orlandini, Cordeiro & Souza (2020: 168).

Phyllanthus saxatilis Strijk & R.W.Bouman nom. nov., homotypic synonym: *Phyllanthus scoparius* Müller (1873: 74), nom. illeg., non *P. scoparius* Welwitsch (1859: 591).

Phyllanthus subgenus **Phyllanthus** section **Choretropsis** Müll.Arg. subsection **Choretropsis**

Phyllanthus subgenus *Phyllanthus* section *Choretropsis* Müll.Arg. subsection *Choretroides* Santiago (2006: 139), *nom. inval.*—Type: *Phyllanthus choretroides* Müll.Arg.

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid; main axis terete or subterete; plagiotropic branchlets terete, cylindrical, clustered at the upper part of the stem or appearing like a much branched shrub with branchlets originated from the base. *Brachyblasts* absent. *Cataphyllary stipules* straight and broadly triangular, entire, apex acuminate or attenuate. *Cataphylls* narrowly triangular, apex acute or acuminate. *Leaves* alternate. *Inflorescences* axillary, unisexual fascicles. *Staminate flowers:* sepals 5 or 6; disc glands 5 or 6; stamens 2 or 3, filaments connate; anthers dehiscing longitudinally (vertically), rarely horizontally. *Pistillate flowers:* sepals 5; disc entire; ovary 3-locular; styles terete, filiform, erect or horizontal, bifid at the upper part. *Fruits* capsules, depressed globose. *Seeds* trigonous, verrucate or finely reticulate.

Distribution: Tropical South America.

Note—Santiago *et al.* (2006) proposed as name of the subsection *Choretroides*, but according to article 22.1 of the ICN (Turland *et al.* 2018), names of subgeneric groups with the type species included are named as autonym without an author cited.

Included species (5 spp.): *P. chapadensis* Orlandini & Silva (in Orlandini *et al.* 2022: 170), *P. choretroides* Müller (1863: 52), *P. goianensis* Santiago (1988: 45), *P. sarothamnoides* Govaerts & Radcliffe-Smith (1996: 177), *P. spartioides* Pax & Hoffmann (*in* Pax 1923: 174).

Phyllanthus L. subgenus **Phyllanthus** section **Loxopodium** G.L.Webster

Phyllanthus L. subgenus *Phyllanthus* section *Loxopodium* Webster (1955: 46); (1956: 346); (1970: 59); (2001b: 380).—Type: *Phyllanthus caroliniensis* Walter.

Synexemia Rafinesque (1825: 2); (1838: 92).—Lectotype (designated here): *Phyllanthus caroliniensis* Walter (formerly *Synexemia caroliniana* Raf.)

Geminaria Rafinesque (1821: 42); (1824: 14).—Type: *Geminaria obovata* Raf. (= *PhylIanthus caroliniensis* Walter).

Phyllanthus L. subgenus *Phyllanthus* section *Salviniopsis* Holm-Nielsen (1979: 279, nom. nud.) ex Brunel (1987: 385).—Type: *Phyllanthus fluitans* Benth. ex Müll.Arg.

Diagnostic features: Annual or perennial herbs or aquatic and *Salvinia*-like, monoecious or dioecious, branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* distichous (blades inflated in *P. fluitans*). *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 3, filaments free, rarely connate at base; anthers subglobose or flattened, dehiscing horizontally; pollen prolate, 3- or 4-colporate, exine with obscure

reticulation. *Pistillate flowers*: sepals 5 or 6; disc cupuliform, lobed or appearing as segments from central ring (*P. hyssopifolioides*); ovary 3-locular; style absent or short; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or verrucate.
Distribution: Americas.

Included species (8 spp.): *P. avicularis* Müller (1863: 32), *P. brandegeei* Millspaugh (1889: 218, as *P. brandegei*), *P. caroliniensis* Walter (1788: 228), *P. evanescens* Brandegee (1905: 207), *P. fallax* Müller (1865a: 377), *P. fluitans* Bentham ex Müller (1863: 36), *P. heliotropus* Wright ex Grisebach (1865: 167), *P. hyssopifolioides* Kunth (1817: 108).

Phyllanthus L. subgenus **Phyllanthus** section **Phyllanthus**

Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus*: Webster (1955: 51); (1957: 295); (1997: 223); (2001b: 386).—*Phyllanthus* section *Euphyllanthus* Baillon (1858: 624), *nom. inval*.; Müller (1863: 3, 22); (1866: 374).—Type: *Phyllanthus niruri* L.

Diagnostic features: Herbs or shrubs, monoecious, branching (sub-)phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular to elongate, usually membranous, sometimes indurate and blackened, base auriculate. *Cataphylls* linear, sometimes leaves not reduced to cataphylls in some species (subsection *Clausseniani*). *Leaves* distichous or subopposite. *Inflorescences* axillary, often unisexual fascicles (spiciform thyrses or racemes at end of branchlets in *P. almadensis*). *Staminate flowers*: sepals (4 or) 5 or 6; disc glandular; stamens (2 or) 3 (or 4), filaments free to completely connate, anther thecae usually not completely separate, sometimes deeply emarginate (appearing stipitate), dehiscing vertically to horizontally; pollen mostly subprolate to prolate, 3- or 4-colporate, exine variously reticulate or tectate-punctate (rarely coarsely reticulate). *Pistillate flowers*: sepals 5 or 6; disc entire or lobed, shallowly cupuliform; ovary 3-locular, glabrous or pubescent; style usuallly absent; stigmas bifid (sometimes only apically emarginate). *Fruits* capsules. *Seeds* trigonous, striate, finely ribbed or verrucate (subsection *Phyllanthus*).

Distribution: Tropical South and Central America, with a pantropical invasive (*P. niruri*).

Note—Herbaceous and small shrubby species of *Phyllanthus* section *Phyllanthus* might prove difficult to distinguish from species of the genus *Moeroris* as they have many similarities in vegetative and floral characters. The subsections of *Phyllanthus* subgenus *Phyllanthus* should be closely compared to species of the genus *Moeroris* to find more distinguishable characters, especially with species such as *M. stipulatus* Raf.

Included species (subsection incertae sedis 3 spp.): *P. carmenluciae* Ribeiro & Loiola (2017: 36), *P. eremitus* Funez & Hassemer (2017: 150), *P. timboensis* Funez, Ferreira & Hassemer (2018: 64).

Phyllanthus L. subgenus **Phyllanthus** section **Phyllanthus** subsection **Almadenses** G.L.Webster

Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus* subsection *Almadenses* Webster (2002a: 5).—Type: *Phyllanthus almadensis* Müll.Arg.

Diagnostic features: Herbs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular, membranous, base not auriculate. *Cataphylls* elongate. *Leaves* subopposite, a single pair per branchlet. *Inflorescences* slender, spiciform thyrses or racemes at end of each branchlet, proximal fascicles staminate, distal ones pistillate. *Staminate flowers*: sepals 5; disc glands 5; stamens 3, filaments free, anthers with enlarged, flattened connective, dehiscing horizontally; pollen prolate, 3-colporate, exine tectate-perforate. *Pistillate flowers*: sepals 5; disc cupular; ovary 3-locular; style absent; stigmas bifid. *Fruits* and *seeds* unknown.

Distribution: Tropical South America.

Included species (1 spp.): *P. almadensis* Müller (1873: 38).

Phyllanthus L. subgenus **Phyllanthus** section **Phyllanthus** subsection **Clausseniani** G.L.Webster

Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus* subsection *Clausseniani* Webster (2002a) 12.—Type: *Phyllanthus claussenii* Müll.Arg.

Diagnostic features: Subshrubs or shrubs, monoecious or dioecious, branching (often sub-) phyllanthoid, pinnatiform (sometimes bipinnatiform in *P. subemarginatus*). *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate or membranous, base not auriculate. *Cataphylls* when present, triangular or linear. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles. *Staminate flowers*: sepals 6; disc glands 6; stamens 3 (2 in *P. allemii*), filaments free (connate in *P. allemii* & *P. fastigiatus*), anthers deeply emarginate with the two thecae often appearing stipitate, dehiscing horizontally; pollen subspheroidal, 4-colporate, exine reticulate (rarely tectate-perforate). *Pistillate flowers*: sepals 6; disc shallowly cupuliform; ovary 3-locular; style absent; stigmas bifid, not capitate. *Fruits* capsules. *Seeds* trigonous, striate or if verrucate/puncticulate then the verruceae in lines.

Distribution: Tropical South America.

Included species (21 spp.): *P. acutifolius* Poiret ex Sprengel (1826: 21), *P. allemii* Webster (2002a: 24), *P. arenicola* Casaretto (1845: 88), *P. atalaiensis* Webster (2002a: 22), *P. blanchetianus* Müller (1863:38), *P. caparaoensis* Webster (2002a: 19), *P. carvalhoi* Webster (2002a: 15), *P. claussenii* Müller (1863: 40), *P. dardanoi* Mendes & Silva (in Mendes *et al.* 2021: 97), *P. fastigiatus* Martius ex Müller (1863: 45), *P. glaziovii* Wallich ex Müller (1873: 41), *P. gongyloides* Cordeiro & Carneiro-Torres (2004: 247), *P. heteradenius* Müller (1873: 63), *P. hypoleucus* Müller (1863: 40), *P. itatiaiensis* Brade (1957: 9), *P. mocotensis* Webster (2002a: 14), *P. piranii* Webster (2002a: 19), *P. retroflexus* Brade (1957: 8), *P. sincorensis* Webster (2002a: 15), *P. subemarginatus* Müller (1863: 39), *P. tuberculatus* Marques-Torres & Silva (2020: 176).

Phyllanthus L. subgenus **Phyllanthus** section **Phyllanthus** subsection **Phyllanthus**

Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus* subsection *Phyllanthus*: Literature and type as under the genus.

Phyllanthus subgenus *Phyllanthus* section *Phyllanthus* subsection *Niruri* Webster (1955: 52); (1957: 299); (1970: 66); (2002a: 2), *nom. inval*.—Type: *Phyllanthus niruri* L.

Diagnostic features: Herbs or undershrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* linear-elliptic, thin and membranous, not auriculate at base. *Cataphylls* linear. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles. *Staminate flowers*: sepals 5 (rarely 6); disc glands 5 or 6; stamens 3, filaments free or connate for 2/3rd, anthers dehiscing obliquely or horizontally; pollen prolate, 4-colporate, exine heteroreticulate. *Pistillate flowers*: sepals 5; disc (shallowly) cupuliform; ovary 3-locular; style absent; stigmas bifid, branch tips subcapitate. *Fruits* capsules. *Seeds* trigonous, verrucate.

Distribution: Tropical South America, West Indies, with one common invasive (*P. niruri*).

Note—Subsection *Niruri* contains the type species of *Phyllanthus*, *P. niruri*, therefore the name should follow the rules for autonyms and become subsection *Phyllanthus*.

Included species (7 spp.): *P. augustinii* Baillon (1865: 354), *P. bolivianus* Pax & Hoffmann (1921: 18), *P. itamarajuensis* Marques-Torres & Silva (2020: 174), *P. longipedicellatus* Silva (2009: 229), *P. mimicus* Webster (1955: 52), *P. niruri* Linnaeus (1753: 981), *P. perpusillus* Baillon (1865: 358).

Phyllanthus L. subgenus **Phyllanthus** section **Pityrocladus** (G.L.Webster) R.W.Bouman, *comb. nov.*

Phyllanthus L. subgenus *Emblica* (Gaertn.) Kurz section *Pityrocladus* Webster (2002: 291).—Type: *Phyllanthus symphoricarpoides* Kunth

Diagnostic features: (Scandent) shrubs, monoecious (rarely dioecious), branchlets rough (scabridulous) to hirtellous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* elongate. *Leaves* distichous. *Inflorescences* axillary, pedicellate, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 (rarely 6); disc glands 5 (rarely 6); stamens 2–5(–7), filaments connate (rarely free), anthers ovoid, dehiscing horizontally or obliquely, connectives non-apiculate; pollen subprolate, 3- or 5-colporate, colpi monoporate, exine reticulate. *Pistillate flowers*: sepals 5; disc cupular or dissected; ovary 3-locular; style absent; stigmas spreading, bifid to entire. *Fruits* capsules (indehiscent in *P. symphoricarpoides*). *Seeds* trigonous, smooth (puncticulate in longitudinal rows in *P. valerii* Standl.).

Distribution: Tropical South and Central America.

Note—*Phyllanthus* section *Pityrocladus* was originally placed in subgenus *Emblica* based on pollen morphology as both groups have species with usually 4- or 5-colporate pollen. However, section *Pityrocladus* is sister to other species of subgenus *Phyllanthus* and is therefore transferred here. Both sections share some palynological characters, but differ slightly in flower morphology (mostly connate versus free stamens).

Included species (6 spp.): *P. cuatrecasanus* Webster (2002b: 292), *P. popayanensis* Pax (1899: 503), *P. ruscifolius* Müller (1866: 358), *P. sponiifolius* Müller (1863: 25), *P. symphoricarpoides* Kunth (1817: 114), *P. valerii* Standley (1937: 619).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers.

Phyllanthus L. subgenus *Xylophylla* (L.) Persoon (1807: 591); Webster (1958: 66).—*Xylophylla* Linnaeus (1771: 147, 221); Swartz (1791: 114, t. 10); de Jussieu (1789: 387); (1824: 23); Gaertner (1790: 123); Rafinesque (1838: 92).—Phy*llanthus* L. section *Xylophylla* (L.) Baillon (1858: 623); Müller (1863: 4, 52); Baillon (1865: 360); Müller (1866: 427); Pax & Hoffmann (1931: 64); Webster (1958: 179).—Lectotype (designated by Webster 1958): *Xylophylla latifolia* L. (= *Phyllanthus epiphyllanthus* L.).

Phyllanthus L. subgenus *Botryanthus* Webster (1956: 345); (1958: 49).—Type: *Phyllanthus grandifolius* L.

Phyllanthus L. section *Typhophyllanthus* Kuntze in Post & Kuntze (1904: 434).—Lectotype (designated here): *Phyllanthus juglandifolius* Willd.

Diagnostic features: Shrubs to trees, monoecious or dioecious, branching phyllanthoid (except in section *Eluanthos*), branchlets (bi)pinnatiform, sometimes transformed into phylloclades, stems rarely ornamented with small platelets. *Brachyblasts* absent. *Cataphyllary stipules* triangular to elongate, indurate, sometimes fusing with cataphylls, base not auriculate. *Cataphylls* triangular to slightly spinescent. *Leaves* usually distichous (except in section *Williamia* subsection *Mirifici*). *Inflorescences* axillary, unisexual or bisexual fascicles, sometimes paniculate. *Staminate flowers*: sepals 4–8; disc entire or 4–6 free glands; stamens 2–7 (up to 15 in section *Williamia*), filaments connate, free or arranged in whorls with varied degree of fusion; anthers usually ovoid, sometimes apiculate, dehiscing horizontally to vertically; pollen spheroidal, clypeate or porate without distinct ectocolpi or colpi anastomosing around exine shields, exine semitectate-reticulate or pilate. *Pistillate flowers*: sepals 4–10; disc entire, sometimes cupuliform, rarely consisting of free glands; ovary 3- or 4(–6)-locular; style present or absent; stigmas free or connate, with bifid to multifid or entire tips, sometimes lacerate, reduced to petaloid structures or fused into a calyptra on top of ovary. *Fruits* capsules or baccate. *Seeds* trigonous or rounded, with or without sarcotesta, smooth or verrucate.

Distribution: Tropical South and Central America, West Indies.

Notes—1. Subgenus *Xylophylla* is one of the more diverse subgenera with a wide variation in both vegetative and floral characters, which makes the group hard to define as a whole.

2. *Phyllanthus* section *Typhophyllanthus* Kuntze was described by Kuntze (1904) as a group that covered five subsections (which are now spread over 4 genera), with very brief morphological descriptions and no types designated. Section *Typhophyllanthus* is placed here into the synonymy of subgenus *Xylophylla* because the characters Kuntze (1904) mentioned only agree with this group. The stamens vary from 5 to 15 in subgenus *Xylophylla* and the genus *Dendrophyllanthus*, but not in the other two genera involved, *Emblica* and *Kirganelia*.

Included species (section incertae sedis 4 spp.): *P. bahiensis* Müller (1863: 20), *P. eurisladro* Martius ex Colla (1836: 106), *P. minarum* Standley & Steyermark (1944: 125), *P. petenensis* Lundell (1985: 367).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Adianthoides** Jabl. ex Jean F.Brunel

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Adianthoides* Jablonski ex Brunel (1987: 236).—Type: *Phyllanthus adianthoides* Klotzsch.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Brachycladus* Webster (2001b: 384).—Type: *Phyllanthus rupestris* Kunth.

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform, short and fasciculate, with only 5–10 leaves per branchlet. *Brachyblasts* absent, but scale-like remnants of previous branchlets present. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles, staminate flowers grouped, pistillate flowers solitary. *Staminate flowers*: sepals 6; disc entire; stamens 3, filaments free or connate, anthers muticous, dehiscence not described; pollen clypeate, pantoporate, exine shields polybrochate. *Pistillate flowers*: sepals 6; disc entire, shallowly cupuliform; ovary 3-locular; style absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth.

Distribution: Tropical South and Central America.

Notes—1. A group with a complicated taxonomy. Brunel (1987) validated two sections within subgenus *Xylophylla* following recommendations by Jablonski (1967). Jablonski (1967) treated several species together in his "*Adianthoides* group", characterized by their free stamens, large leaves, short globular anthers and bifid styles, and proposed *P. francavillanus* Müller (1863: 20) and *P. adianthoides* Klotzsch as possible types. Jablonksi numbered the species in his treatment and wished to include numbers 20–33, thereby strangely excluding *P. adianthoides* (number 38). *Phyllanthus adianthoides* does not match with its connate stamens (as opposed to free in the others). Even though Brunel (1987) published Jablonski's *Adianthoides* group as two separate sections, the group was found to be heterogenous in other treatments (Webster 1999, 2001b, 2004). *Phyllanthus francavillanus* was reduced to a subspecies of *P. myrsinites* Kunth (Webster 1999) and its section is considered a heterotypic synonym of *Phyllanthus* subgenus *Microglochidion*. Section *Adianthoides*, as circumscribed here, was included by Webster's (2001b) section *Brachycladus* G.L.Webster. The descriptions of both sections overlap greatly (mainly in the entire staminate disc and areolate pollen), but differ in the staminal fusion (strictly free (Brunel 1987) versus free or connate (Webster 2001b)). These two sections should logically be combined as Webster (2001b) already treated all the included species together, but perhaps thought that the group was not officially published yet. Since section *Adianthoides* is the older name, section *Brachycladus* is placed in its synonymy.

2. While branchlets are fascicled, they can appear as bipinnatiform branchlets (see *P. spruceanus* Müll.Arg.), which occurs in more sections of subgenus *Xylophylla*.

Included species (7 spp.): *P. adianthoides* Klotzsch (1843: 51), *P. atabapoensis* Jablonski (1967: 110), *P. borjaensis* Jablonski (1967: 108), *P. mickelii* McVaugh (1961: 196), *P. paezensis* Jablonski (1967: 113), *P. rupestris* Kunth (1817: 110), *P. spruceanus* Müller (1863: 40).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Asterandra** (Klotzsch) Müll.Arg.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Asterandra* (Klotzsch) Müller (1863: 2, 5); Baillon (1865: 360); Müller (1866: 329); Webster (1958: 146).—*Asterandra* Klotzsch (1841: 200); Baillon. (1858: 610).—*Phyllanthus* L. section *Typhophyllanthus* Kuntze subsection *Asterandra* (Klotzsch) Kuntze in Post & Kuntze (1904: 434).—Type: *Asterandra cornifolia* (Kunth) Klotzsch (= *Phyllanthus juglandifolius* Willd.)

Diagnostic features: Shrubs or trees, monocaulous, monoecious, branching phyllanthoid, branchlets pinnatiform, clustered at apex. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, mostly bisexual fascicles, usually more pistillate flowers at proximal nodes and distally more staminate flowers. *Staminate flowers*: sepals 5; disc entire, 5-angled, segments coalescent into a massive ring, pentagonal, indented at anthers; stamens 3–7, filaments and connectives connate, anthers ovoid, flattened, dehiscing horizontally or slightly reflexed; pollen clypeate, exine reticulate. *Pistillate flowers*: sepals 5 (or 6); disc entire, massive, 5-angled; ovary 3-locular, carinate; style present; stigma tips bifid or emarginate, triangular, petaloid. *Fruits* capsules. *Seeds* globose, woody, smooth, with a mottled pattern.

Distribution: Tropical South America and West Indies.

Included species (2 spp.): *P. gentryi* Webster in Webster & Huft (1988: 1096), *P. juglandifolius* Willdenow (1814: 64).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Callitrichoides** (G.L.Webster) Jean F.Brunel

Phyllanthus L. subgenus *Microglochidion* (Müll.Arg.) Jean F.Brunel section *Callitrichoides* (Webster 1955: 47) Brunel (1987: 237).—*Phyllanthus* L. subgenus *Phyllanthus* section *Callitrichoides* Webster (1957: 171).—*Phyllanthus* subgenus *Cyclanthera* G.L.Webster section *Callitrichoides* (G.L.Webster) Webster (2002b: 295).—Type: *Phyllanthus carnosulus* Müll.Arg.

Diagnostic features: Perennial diminutive herbs, monoecious, branching phyllanthoid, main axes from a small rootstock, branchlets pinnatiform and clustered at apex, sometimes rooting at the nodes. *Brachyblasts* absent. *Leaves* distichous, slightly succulent. *Inflorescences* axillary, unisexual fascicles (or flowers solitary). *Staminate flowers*: sepals 5; disc glands 5, purplish; stamens 2, filaments connate; anthers globular, dehiscing horizontally, extrorse, connectives not apiculate; pollen spheroidal, exine with band-shaped shields. *Pistillate flowers*: sepals 6; disc glands

6, free, purplish; ovary 3-locular; style absent; stigma tips bifid or emarginate. *Fruits* capsules, surface rough. *Seeds* trigonous, verrucate.

Distribution: West Indies (Cuba).

Note—Though *P. carnosulus* Müll.Arg. is yet to be included in any phylogenetic study, a species resembling section *Callitrichoides* was found to be nested within subgenus *Xylophylla* (Falcón *et al.* 2020). Webster's (2002) suggestion that the pollen of *Phyllanthus* section *Callitrichoides* can be inferred as stephanocolporate is in line with Brunel's (1987) decision to place this section in subgenus *Microglochidion*. Webster (1957) originally interpreted the pollen as having elongated exine shields, which might prove to be an intermediate between the stephanocolporate pollen of subgenus *Microglochidion* and the clypeate pollen of subgenus *Xylophylla*.

Included species (1 sp.): *P. carnosulus* Müller (1863:30).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Cyclanthera** (G.L.Webster) Jean F.Brunel

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Cyclanthera* (G.L.Webster) Brunel (1987: 234).—*Phyllanthus* L. subgenus *Phylllanthus* section *Cyclanthera* Webster (1955: 47).—*Phyllanthus* L. subgenus *Cyclanthera* (G.L.Webster) Webster (1957: 177); (2002b: 295).—Type: *Phyllanthus lindenianus* Baill.

Diagnostic features: Annual or perennial herbs or subshrubs, monoecious, branching phyllanthoid, branchlets pinnatiform (sometimes bipinnatiform). *Brachyblasts* absent. *Cataphyllary stipules* triangular-ovate, membranous, base not auriculate. *Cataphylls* elliptic. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles (or flowers solitary). *Staminate flowers:* sepals 5 or 6; disc glands 5 or 6, free; stamens 2 or 3, filaments connate, anthers completely connate into a disciform circumsessile synandrium, connectives fused and not apiculate; pollen spheroidal, pantoporate, exine honey-comb like clypeate, shields roundish with a single central pilum. *Pistillate flowers:* sepals 6; disc glands 6, free, often purplish; ovary 3-locular; style present or absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous verrucate.

Distribution: West Indies (Cuba, Dominican Republic, Haiti).

Notes—1. *Phyllanthus* subgenus *Cyclanthera* was found to be nested within *Phyllanthus* subgenus *Xylophylla* (Falcón *et al.* 2020; Bouman *et al.* 2020). This group of species was originally treated as a section within subgenus *Phyllanthus* and later transferred to *Phyllanthus* subgenus *Xylophylla* (Brunel 1987), before gaining its own subgeneric status (Webster 2002b). The easiest solution seems to be to revert back to Brunel's (1987) decision to retain section *Cyclanthera* within *Phyllanthus* subgenus *Xylophylla*.

2. Webster & Carpenter (2002) provided several theories to explain the origin of the unique pollen morphology of *P. lindenianus* Baill. Affinities to *Phyllanthus* subgenus *Conami* and *Xylophylla* were discussed and section *Cyclanthera* was shown to be nested within the latter group. A close relationship between *Phyllanthus* subgenus *Conami* section *Apolepsis* was also discussed, but this species has yet to be included in a phylogenetic study. However, the absence of muri in the pollen of section *Apolepsis* (Webster & Carpenter 2002) argues against a close relationship, since this would indicate an even more drastic reduction of the clypeate pollen in *Phyllanthus* subgenus *Xylophylla*.

Included species (4 spp.): *P. abditus* Webster (1955: 50), *P. berteroanus* Müller (1863: 44), *P. lindenianus* Baillon (1861: 13), *P. tenuicaulis* Müller (1863: 44).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Diplocicca** Müll.Arg.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Diplocicca* Müller (1873: 30); Pax & Hoffmann (1931: 62).—Type: *Phyllanthus octomerus* Müll.Arg.

Diagnostic features: Shrubs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles, staminate flowers in fascicles on proximal part of branchlets, pistillate flowers more distal and solitary. *Staminate flowers*: sepals 6–8; disc entire; stamens 3 or 4, filaments free, anthers dehiscing vertically, connectives non-apiculate; pollen spheroidal, clypeate, exine shields oligobrochate, reticulate. *Pistillate flowers*: sepals 8–10; disc shallowly cupuliform; ovary 4-locular; style absent; stigmas bifid. Fruits and seeds not known.

Distribution: Tropical South America.

Included species (1 sp.): *P. octomerus* Müller (1873: 30).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Elutanthos** Croizat

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Elutanthos* Croizat (1943b: 12); Brunel (1987: 234).—*Phyllanthus* L. subgenus *Botryanthus* G.L.Webster section *Elutanthos* (Croizat) Webster (1956: 345); (1958: 50).—Type: *Phyllanthus glaucescens* Kunth (= *P. grandifolius* L.)

[*Phyllanthus* L. section *Glochidionanthus* Baillon (1865: 359, nom. nud.]

Diagnostic features: Shrubs or trees, monoecious, branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles or thyrses (sometimes racemose and seemingly at end of branches). *Staminate flowers*: sepals 6; disc glands 6, often massive; stamens (2 or) 3, filaments connate; anthers deflexed, dehiscing more or less horizontally, connectives non-apiculate (except in *P. urbanianus* Mansf.); pollen globose, clypeate, exine semitectate-reticulate. *Pistillate flowers*: sepals 6; disc shallowly cupuliform, usually foveolate or crenulate; ovary 3-locular; style present; stigmas erect, entire to bifid. *Fruits* capsules, obscurely rugulose. *Seeds* trigonous, smooth.

Distribution: Tropical South America and West Indies.

Included species (24 spp.): *P. adenodiscus* Müller (1863: 23), *P. anderssonii* Müller (1866: 395), *P. biantherifer* Croizat (1944: 7), *P. botryanthus* Müller (1866: 323), *P. chiapensis* Sprague (1909: 264), *P. cladotrichus* Müller (1863: 25), *P. coalcomanensis* Croizat (1943b: 13), *P. gradyi* Silva & de Sales (2006: 421), *P. grandifolius* Linnaeus (1753: 981), *P. huallagensis* Standley ex Croizat (1943b: 13), *P. laxiflorus* Bentham (1842: 90), *P. mutisianus* Webster (2001a: 65), *P. nutans* Swartz (1788: 27), *P. oaxacanus* Brandegee (1915: 185), *P. pachystylus* Urban (1902: 286), *P. poeppigianus* (Müller 1863: 71) Müller (1866: 323), *P. racemiger* Müller (1863: 23), *P. ramosus* Vellozo (1831: pl. 17), *P. tequilensis* Robinson & Greenman (1894: 392), *P. umbratus* Müller (1866: 356), *P. urbanianus* Mansfeld (1933: 86), *P. ventricosus* Webster (1967a: 198), *P. vincentae* Macbride (1951: 47), *P. zanthoxyloides* Steyermark in Steyermark *et al.* (1952: 321).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Epistylium** (Sw.) Griseb.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Epistylium* (Sw.) Grisebach (1859: 33); Müller (1863: 3, 46); (1866: 412); Pax & Hoffmann (1931: 65); Webster (1958: 153).—*Epistylium* Swartz (1800: 1099); de Jussieu (1824: 17); Baillon (1858: 645).—Lectotype (designated by Webster 1958): *Epistylium axillare* (Sw.) Sw. (= *Phyllanthus axillaris* (Sw.) Müll.Arg.).

Phyllanthus L. section *Catastylium* Grisebach (1859: 33); Müller (1866: 413); Pax & Hoffmann (1931: 64).—Lectotype (designated here): *Phyllanthus cauliflorus* (Sw.) Griseb.

Diagnostic features: Shrubs or (monocaulus) trees, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform, clustered at the apex of the more or less unbranched stem. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary or cauliflorous thyrses, bisexual fascicles. *Staminate flowers*: sepals 4 or 5; disc glands 4 or 5; stamens 2 or 3, filaments connate; anthers deflexed, dehiscing longitudinally and obliquely (downward) to horizontally; pollen spheroidal, clypeate, exine reticulate. *Pistillate flowers*: receptacle and calyx massive, sepals 5, erect; disc indistinct, lobed or consisting of 5 glands; ovary subglobose to beaked; style absent; stigmas petaloid, massive, often reflexed at top of ovary or at end of elongated ovarial beak (*P. cauliflorus*). *Fruits* capsules, angled. *Seeds* 1 (by abortion) or 2 per locule, smooth.

Distribution: West Indies.

Included species (3 spp.): *P. axillaris* (Swartz 1788: 95) Müller (1866: 412), *P. cauliflorus* (Swartz 1788: 95) Grisebach (1859: 33), *P. cladanthus* Müller (1863: 46).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Glyptothamnus** G.L.Webster

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Glyptothamnus* Webster (1958: 68, 160).—Type: *Phyllanthus chryseus* R.A.Howard.

Diagnostic features: Treelet-like shrubs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous, margins distinctly revolute and thickened. *Inflorescences* axillary, mostly unisexual fascicles, but staminate and pistillate flowers ± interspersed. *Staminate flowers*: sepals 4; disc entire, massive; stamens 2, filaments and connectives connate, anthers dehiscing horizontally; pollen clypeate, exine reticulate. *Pistillate flowers*: sepals 5; disc entire, massive; ovary 3-locular; style absent; stigmas spreading, dilated, lacerate. *Fruits* capsules, globose, not sulcate (grooved). *Seeds* trigonous, dark, fissured.

Distribution: West Indies (Cuba).

Included species (1 sp.): *P. chryseus* Howard (1947: 121).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Hylaeanthus** (G.L.Webster) R.W.Bouman, *comb. nov.*

Phyllanthus L. subgenus *Conami* (Aubl.) G.L.Webster section *Hylaeanthus* Webster (2002b: 293); (2004: 12).—Type: *Phyllanthus attenuatus* Miq.

Meborea Aublet (1775: 825, t 323); Baillon (1858: 656).—Type: *Meborea guianensis* Aubl. (= *Phyllanthus attenuatus* Miq.).

Diagnostic features: Mostly trees, sometimes shrubs, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform (sometimes fascicled on slender permanent stalk), usually subtended by reduced leaves (but generally not reduced to cataphylls), sometimes lenticellate. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual (rarely bisexual) fascicles, sometimes supra-axillary. *Staminate flowers*: sepals 6 (rarely 5), in two whorls; disc entire and 6-lobed or less often divided into glands; stamens 3, filaments connate (free in *P. skutchii* Standl.); anthers muticous, dehiscing horizontally or obliquely; pollen globose (spheroidal), porate, lacking distinct ectocolpi, exine pilate, heterogenous. *Pistillate flowers*: sepals 6; disc shallowly cupuliform to cupular; ovary 3–6-locular; style present or absent; stigmas bifid to entire. *Fruits* baccate, with fleshy exocarp. *Seeds* smooth, with sarcotesta.

Distribution: Tropical South America.

Note—The apparent relationship between sections *Hylaeanthus* and *Adianthoides* indicated a separate loss of clypeate pollen (discussed in Bouman *et al.* 2021). The difference in pollen morphology is quite surprising as section *Adianthoides* has clypeate pollen with reticulate exine (as is standard for subgenus *Xylophylla*) while pollen of species in section *Hylaeanthus* is simply porate with no colpi and pilate exine (more common in subgenus *Conami*). The differences in pollen morphology are striking and possibly reflect independent origins of the pilate exine within *Phyllanthus*. These groups do show agreement in vegetative characters (see Webster 2002b) and in the morphology of the staminate flower. Both groups have species with usually three stamens and an entire disc.

Included species (8 spp.): *P. attenuatus* Miquel (1848: 479), *P. awaensis* Webster (2004: 24), *P. bernardii* Jablonski (1967: 112), *P. callejasii* Webster (2002b: 295), *P. madeirensis* Croizat (1944: 7), *P. puntii* Webster (2004: 21), *P. skutchii* Standley (1940: 346), *P. valleanus* Croizat (1946: 354).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Orbicularia** (Baill.) Griseb.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Orbicularia* (Baillon 1858: 616) Grisebach (1859: 34); Müller (1863: 2, 5); (1866: 331); Pax & Hoffmann (1931: 62); Webster (1958: 111).—*Orbicularia* Baillon (1858: 616).—Type: *Orbicularia phyllanthoides* Baill., nom. illeg. (= *Phyllanthus orbicularis* Kunth).

Williamia Baillon (1858: 559).—*Phyllanthus* L. subgenus *Xylophylla* (L.) Pers. section *Williamia* (Baill.) Müller (1863: 2, 4); (1866: 328); Pax & Hoffmann (1931: 61); Webster (1958: 69).—Type: *Williamia pruinosa* Baill. (= *Phyllanthus discolor* Poepp. ex Spreng.).

Dimorphocladium Britton (1920: 74).—Type: *Dimorphocladium formosum* (Urb.) Britton (= *Phyllanthus formosus* Urb.).

Roigia Britton (1920: 73).—*Phyllanthus* L. section *Dimorphocladium* (Britton) Pax & Hoffmann (1931: 63).—Type: *Roigia comosa* (Urb.) Britton (= *Phyllanthus comosus* Urb.).

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Williamia* (Baill.) Müll.Arg. subsection *Discolores* Webster (1958: 71).—Type: *Phyllanthus discolor* Poepp.

Diagnostic features: Shrubs or small trees, monoecious, branching phyllanthoid (sub-phyllanthoid in *P. formosus*), branchlets pinnatiform. *Brachyblasts* absent. *Inflorescences* axillary, bisexual or unisexual fascicles or with solitary flowers. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6, free or coalescent; stamens 3–7(–15 in *P. discolor* and *P. microdictyus* Urb.), in two whorls, filaments completely or partially connate, can be massive and then whorled

on central pillar, anthers dehiscing horizontally or obliquely (sometimes a part of the stamens dehiscing vertically), connectives sometimes apiculate; pollen spheroidal, clypeate, exine shields oligobrochate, reticulate. *Pistillate flowers*: sepals 5 or 6 (or rarely 7 in *P. microdictyus*); disc tenuous to rather massive, sometimes 5-angled (fused with gynophore in *P. microdictyus*); ovary 3-locular, sessile or definitely stipitate (gynophore); style present or absent; stigma tips bifid, often revolute, moderately dilated distally, tips variable from crescent-shaped to lacerate and 4-tipped. *Fruits* oblate capsules, veins conspicuous or obscure. *Seeds* trigonous, verrucate (with longitudinal lines or dark reddish brown dots in *P. discolor*, puncticulate in *P. cristalensis* Urb.).

Distribution: West Indies.

Note—Webster (1958) described three subsections for section *Williamia* (*Discolores*, *Incrustati* and *Mirifici*), that were differentiated based on stem ornamentation and phyllotaxy. *Phyllanthus* subsection *Discolores* contains the type species of section *Williamia* and it is found here to be paraphyletic with species of *Phyllanthus* section *Orbicularia* (Supplementary Fig. 1). Subsection *Discolores* is merged here with section *Orbicularia*. The two other subsections previously placed in Webster's (1958) definition of section *Williamia*, form a monophyletic group (Supplementary Fig. 1) and these are treated here as the reinstated section *Williamiandra* (see below).

Included species (13 spp.): *P. chamaecristoides* Urban (1924: 185), *P. comosus* Urban (1914: 451), *P. cristalensis* Urban (1930: 212), *P. cuneifolius* Britton (1920: 72) Croizat (1943b: 12), *P. discolor* Poeppig ex Sprengel (1826: 21), *P. formosus* Urban (1914: 450), *P. microdictyus* Urban (1924: 18), *P. myrtilloides* Grisebach (1860: 158), *P. nummularioides* Müller (1863: 5), *P. orbicularis* Kunth (1817: 111), *P. phialanthoides* Falcón & J.L.Gómez in Falcón *et al.* (2017: 2), *P. phlebocarpus* Urban (1924: 189), *P. scopulorum* (Britton 1920: 72) Urban (1924: 187).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Oxalistylis** Baill.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Oxalistylis* Baillon (1858: 628); Müller (1863: 2, 5); Baillon (1865: 359); Müller (1866: 330); Pax & Hoffmann (1931: 62).—Type: *Phyllanthus salviifolius* Kunth.

Diagnostic features: Shrubs, sometimes arborescent, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* and *cataphylls* not seen. *Leaves* distichous. *Inflorescences* axillary, mostly unisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5; stamens 3–7, filaments connate, anthers dehiscing ± horizontally; pollen clypeate, exine reticulate. *Pistillate flowers*: sepals 6; disc entire; ovary 3-locular; style present; stigmas elongated and exserted from calyx, tips dilated, bifid to multifid. *Fruits* capsules. *Seeds* trigonous, smooth.

Distribution: Tropical South America.

Included species (1 sp.): *P. salviifolius* Kunth (1817: 116).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Thamnocharis** G.L.Webster

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Thamnocharis* Webster (1955: 59); (1958: 91).—Type: *Phyllanthus cinctus* Urb.

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles, flowers appearing with the expanding leaves. *Staminate flowers*: sepals 4 (6, rarely 5 in *P. comptus* G.L.Webster); disc glands 4 (6, rarely 5 in *P. comptus*); stamens 2 (4–8 in *P. comptus*), filaments connate (but free in *P. comptus*), anthers dehiscing vertically; pollen spheroidal, clypeate, exine reticulate. *Pistillate flowers*: sepals 4 (6, rarely 5 in *P. comptus*); disc entire, angled; ovary 3-locular; style absent or present (and elongated); stigmas bifid, tips narrowed to acute. *Fruits* capsules, subglobose. *Seeds* trigonous, smooth or rugulose.

Distribution: West Indies (Cuba).

Note—Differences and similarities with *Nymphanthus acutissimus* were discussed at length by Webster (1955). Vegetatively, these groups can be distinguished by the smaller persistent stipules and thinner leaves in *Nym. acutissimus*. In contrast with section *Thamnocaris*, the inflorescences in *Nym. acutissimus* are unisexual, the pistillate flowers usually have six sepals and the ovary is verrucate.

Included species (3 spp.): *P. cinctus* Urban (1924: 191), *P. comptus* Webster (1955: 61), *P. ekmanii* Webster (1955: 60).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Williamiandra** (Griseb.) R.W.Bouman, *stat. nov*.

Phyllanthus L. section *Williamiandra* Grisebach (1865: 169).—*Phyllanthus* L. subgenus *Xylophylla* (L.) Pers. section *Williamia* (Baill.) Müll.Arg. subsection *Incrustati* Webster (1958: 82).—Type: *Phyllanthus williamioides* Griseb.

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform, stems sometimes ornamented with small platelets or smooth and lenticellate. *Brachyblasts* absent. *Leaves* alternate or opposite, distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5; stamens (2 or) 3 or 5, filaments connate, anthers inserted at the top or in two close whorls (see Webster 1958), anthers vertically to horizontally dehiscing, connectives sometimes apiculate; pollen clypeate, exine reticulate. *Pistillate flowers*: sepals 5–7; disc entire, angular, often massive; ovary 3-locular, sessile or definitely stipitate (gynophore); style present or absent; stigmas with tips dilated and lacerate or dentate. *Fruits* capsules, oblate, dry, not veiny. *Seeds* trigonous, colliculose or verrucate, verrucae < 3 mm high.

Distribution: West Indies.

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Williamiandra** Griseb. subsection **Mirifici** (G.L.Webster) R.W.Bouman, *comb. nov*.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Williamia* (Baill.) Müll.Arg. subsection *Mirifici* Webster (1958: 89).—Type: *Phyllanthus mirificus* G.L.Webster

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform, axes smooth but prominently lenticellate. *Brachyblasts* absent. *Leaves* opposite. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5; stamens 5, filaments connate, 2 anthers inserted lower than the other 3, dehiscing more or less vertically. *Pistillate flowers*: sepals 6; disc entire, massive, bluntly angled; ovary 3-locular; style present or absent; stigmas with lower margins reflexed, dilated and covering the ovary, forming a close fitting cap. *Fruits* and *seeds* unknown.

Distribution: West Indies.

Included species (1 sp.): *P. mirificus* Webster (1955: 58).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Williamiandra** Griseb. subsection **Williamiandra**

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Williamiandra*: Literature and type as under the section.
Ramsdenia Britton (1920: 72).—Type: *Ramsdenia incrustata* (Urb.) Britton (= *Phyllanthus incrustatus* Urb.).

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform, all axes incrustate with dark platelets of bark, dark or reddish brown to black. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5; stamens (2 or) 3–6, filaments connate in a column, anthers sometimes in 2 whorls (2 sets on top of column), dehiscing longitudinally, vertically and horizontally often in same flower, connectives sometimes apiculate. *Pistillate flowers*: sepals 5–7, unequal; disc entire, massive, sometimes 5-angled; ovary 3-locular; style present or absent; stigmas with conspicuously lacerate endings of 3–6 tips. *Fruits* capsules. *Seeds* trigonous, smooth or with carinate back.

Distribution: West Indies (Cuba).

Included species (3 spp.): *P. excisus* Urban (1914: 449), *P. incrustatus* Urban (1914: 449), *P. williamioides* Grisebach (1865: 169).

Phyllanthus L. subgenus **Xylophylla** (L.) Pers. section **Xylophylla**

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Xylophylla*: Literature and type as under the subgenus.
Genesiphylla L'Héritier de Brutelle (1778: 29); Rafinesque (1838: 92.—*Phyllanthus* L. section *Typhophyllanthus* Kuntze subsection *Genesiphylla* (L'Hér.) Kuntze in Post & Kuntze (1904: 434).—Type: *Genesiphylla asplenifolia* L'Hér., nom. illeg. (= *Xylophylla latifolia* L. = *Phyllanthus epiphyllanthus* L.).

Hexadena Rafinesque (1838: 92).—Type: *Hexadena angustifolia* (Sw.) Raf. (= *Phyllanthus angustifolius* (Sw.) Sw.).

Glochidion J.R.Forst. & G.Forst. section *Hemiphyllanthus* Müller (1863: 59, 71); Pax & Hoffmann (1931: 58).—*Phyllanthus* L. section *Hemiphyllanthus* (Müll. Arg.) Müller (1865a: 370); (1866: 323).—*Phyllanthus* L. subgenus *Xylophylla* (L.) Pers. section *Hemiphyllanthus* (Müll.Arg.) Webster (1955: 62); (1958: 163).—Lectotype (designated by Webster 1955): *Phyllanthus ovatus* Poir.

Diagnostic features: Shrubs or small trees, monoecious, branching phyllanthoid, branchlets (bi)pinnatiform with ultimate axes transformed into broad or thin phylloclades. *Brachyblasts* absent. *Leaves* either reduced to scales or well-developed. *Inflorescences* axillary, unisexual or bisexual fascicles at nodes of phylloclades. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 2–6, filaments united at least at the base, anthers dehiscing more or less horizontally; pollen globose, clypeate, exine shields oligobrochate, reticulate. *Pistillate flowers*: sepals 5 or 6; disc segmented to urceolate; ovary 3-locular; style present or absent; stigmas often lobed or bifid, sometimes reduced to short projections from ovary (*P. megapodus* Webster 1955: 62). *Fruits* capsules, oblate, smooth to tuberculate. *Seeds* trigonous or sometimes (when 1 locule developed) ovate and flattened, verrucate (or smooth in *P. maleolens* Urb. & Ekman).

Distribution: West Indies.

Notes—1. The genus *Lomanthes* Raf. was listed as a synonym of section *Xylophylla* in Webster (1958), but with no re-identification of the type. The type species is listed on The Plant List (2013) as *P. hirtellus* (here *Lysiandra hirtellus*), an Australian endemic, which seems strange considering *Lomanthes* was described from North America. On Index Nominum Genericorum (Farr & Zijlstra 1996), *Lomanthes latifolia* is listed as a synonym of *P. epiphyllanthus*. We have not seen the type material and cannot correctly conclude where this name should be placed.

2. Webster (1956, 1958: 180) selected *Xylophylla latifolia* as the type species for section *Xylophylla* and selected a lectotype for the species. A later typification for section *Xylophylla* with as type *Xylophylla longifolia* (Jarvis *et al.* 1993) as listed in the Index Nominum Genericorum (Farr & Zijlstra 1996) is superfluous.

3. *Phyllanthus* section *Hemiphyllanthus* was found to be nested within a paraphyletic section *Xylophylla* (Bouman *et al.* 2021). Section *Hemiphyllanthus* is very similar to section *Xylophylla* as the branchlets appear like thin phylloclades that still produce laminate leaves. However, there is no trace that the branchlets evolved from an ancestor with bipinnatiform branchlets. Both sections are here combined with as synapomorphy the transformation of branchlets into phylloclades, with or without laminate leaves.

Included species (16 spp.): *P. acacioides* Urban (1902: 287), *P. angustifolius* (Swartz 1788: 28) Swartz (1800: 1111), *P. arbuscula* (Swartz 1788: 28) Gmelin (1791: 204), *P. epiphyllanthus* Linnaeus (1753: 981), *P. eximius* Webster & Proctor in Webster (1960: 283), *P. latifolius* (Linnaues 1771: 221) Swartz (1800: 1109), *P. maleolens* Urban & Ekman in Urban (1928: 60), *P. martii* Müller (1873: 27), *P. megapodus* Webster (1955: 62), *P. mimosoides* Swartz (1788: 27), *P. montanus* (Swartz 1788: 28) Swartz (1800: 1117), *P. myriophyllus* Urban (1921: 36), *P. obtusatus* (Thunberg 1817: 12) Müller (1866: 433), *P. ovatus* Poiret (1804: 297), *P. proctoris* Webster (1958: 195), *P. robustus* Martius ex Colla (1836: 106).

Clade F—Figs. 1, 2J & K (supplementary fig. 1)

Cicca L.

Cicca Linnaeus (1767: 124); de Jussieu (1789: 386); (1824: 20); Baillon (1858: 617); Robinson (1909: 87); Ridley (1924: 216).—*Phyllanthus* L. section *Cicca* (L.) Müller (1863: 3, 50); (1866: 413); Hooker (1887: 287); Boerlage (1900: 213); Pax & Hoffmann (1931: 62).—*Phyllanthus* L. subgenus *Eucicca* Kurz (1873: 238), *nom. inval*.—*Phyllanthus* L. subgenus *Cicca* (L.) Webster (1957: 60); Brunel (1987: 289).—*Phyllanthus* L. subgen. *Kirganelia* (A.Juss.) Kurz section *Cicca* (L.) Webster (2001b: 381).—Type: *Cicca disticha* L. (= formerly synonym of *Phyllanthus acidus* (L.) Skeels) = *Cicca acida* (L.) Merr.

Tricarium de Loureiro (1790: 557).—Type: *Tricarium cochinchinense* Lour. (= formerly synonym of *Phyllanthus acidus* (L.) Skeels = *Cicca acida* (L.) Merr.).

Staurothyrax Griffith (1854: 476).—Type: Not designated (only a *S. spec.* described).

Phyllanthus L. subgenus *Ceramanthus* (Hassk.) Jean F.Brunel section *Ebolowani* Brunel (1987: 412). – Type: *Phyllanthus letouzeyanus* Jean F.Brunel. = *Cicca letouzeyanus* (Jean F.Brunel) R.W.Bouman.

Diagnostic features: Herbs, shrubs or trees, monoecious or dioecious, branching (non-)phyllanthoid, branchlets (bi)pinnatiform (sometimes further ramified), rarely opposite (subgenus *Menarda* (Comm. ex A.Juss.) R.W.Bouman), sometimes specialized in vegetative and floriferous branchlets. *Brachyblasts* present or absent. *Cataphyllary stipules* triangular or spinescent, indurate or membranous, base usually not auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous to opposite, sometimes spiral at base. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 4–6; disc entire or 4–6 glands, sometimes absent; stamens 2–6, filaments mostly free, sometimes (basally) connate, basifixed or connate (in some species of subgenus *Menarda*); anthers dehiscing longitudinally, vertically to obliquely to horizontally, connectives (non-)apiculate; pollen spheroidal or oblate, 3- or 4-(syn)colporate, colpi monoporate (to diploporate in subgenus *Menarda*), exine reticulate (or perforate in subgenus *Menarda*); pistillode absent. *Pistillate flowers*: sepals 4–6; disc entire, segmented or absent; ovary 2–4-locular; styles present or absent; stigmas entire or bifid. *Fruits* baccate or capsular. *Seeds* trigonous to rounded or reniform, sometimes with cavity at hilum, smooth or with minute striae.

Distribution: Africa, Madagascar, Asia, Malesia, Pacific, South America.

Notes—1. The genus *Cicca* is here reinstated, but considerably expanded in comparison to its original circumscription. This genus was created because the type species was very different from known *Phyllanthus* species. Based on fruit morphology, this genus has also been mixed with species of *Emblica* and *Margaritaria*. In our treatment, we consider a wider circumscription that includes former *Phyllanthus* subgenera *Anesonemoides*, *Betsileani* and *Menarda* as these were shown to be closely related (see Bouman *et al.* 2020; supplementary fig. 1). This clade was found to be sister to the diverse genus *Dendrophyllanthus* here (but see Kawakita *et al.* 2009).

2. The monotypic section *Ebolowani* was placed by Brunel (1987) in *Phyllanthus* subgenus *Ceramanthus* (here genus *Cathetus*) on the basis of a vague similarity in exine morphology. However, this species has phyllanthoid branching (vs non-phyllanthoid in the genus *Cathetus*) and staminate flowers with free stamens (connate in *Cathetus* subgenus *Cathetus*). The anther shape of *Cicca letouzeyanus* differs considerably from *Cathetus* subgenus *Macraea*, therefore we consider placing this species in *Cathetus* to be incorrect. There is no species in Africa with a close morphological affinity to *Cicca letouzeyanus*. A macroreticulate exine is also found in some species of *Moeroris*, but the species of that genus usually have connate stamens (or free in *Moeroris* subgenus *Tenellanthus*, but then the flower is usually 5-merous). Free stamens and a small-tree like habit is more common in the genus *Cicca*. However, the exact subgenus for *C. letouzeyanus* is unclear, so we transfer this species to the genus *Cicca* without any subgeneric placement. If the species is shown to be phylogenetically distinct, section *Ebolowani* could be reinstated again.

Included, but further unplaced species and taxonomic changes (3 spp.):

Cicca analamerae (Leandri 1957: 225) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus analamerae* Leandri.

Cicca letouzeyanus (Brunel 1987: 409) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus letouzeyanus* Jean F.Brunel.

Cicca vergens (Baillon *in* Grandidier 1892: pl. 225) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vergens* Baill.

Cicca L. subgenus **Anisonemoides** (Jean F.Brunel) R.W.Bouman, *comb. nov.*

Phyllanthus L. subgenus *Anisonemoides* (Jean F.Brunel) Ralimanana & Hoffmann (2014: 267).—*Phyllanthus* L. subgenus *Kirganelia* (A.Juss.) Kurz section *Anisonemoides* Brunel (1987: 276).—Type: *Phyllanthus bojerianus* (Baill.) Müll.Arg. (based on *Kirganelia bojeriana* Baill.) = *Cicca bojeriana* (Baill.) R.W.Bouman.

Diagnostic features: Shrubs, subshrubs or small trees, monoecious or dioecious, branching phyllanthoid, branchlets (bi)pinnatiform. *Brachyblasts* absent (rarely present). *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles, rarely bisexual, not on separate branchlets. *Staminate flowers*: sepals (4)5(6); disc glands (4)5(6); stamens (2–4)5(6), filaments free or inner ones tending to be fused, anthers dehiscing longitudinally, connectives non-apiculate; pollen 3-colporate or 3-syncolporate, colpi monoporate, exine macro- or microreticulate. *Pistillate flowers*: sepals 5 or 6; disc entire; ovary 3-locular; styles absent or present; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or faintly longitudinally striate.

Distribution: Africa, Madagascar.

Included species and taxonomic changes (13 spp.):

Cicca ambatovolana (Leandri 1938: 191) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ambatovolanus* Leandri.

Cicca ankarana (Leandri 1934: 543) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ankarana* Leandri.

Cicca bemangidiensis (Ralimanana *in* Ralimanana & Hoffmann 2014: 285) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bemangidiensis* Ralim.

Cicca bojeriana (Baillon 1861: 47) R.W.Bouman, *comb. nov.* Basionym: *Kirganelia bojeriana* Baill., synonym: *Phyllanthus bojerianus* (Baill.) Müll.Arg. (1866: 343).

Cicca gordonii (Ralimanana *in* Ralimanana & Hoffmann 2014: 276) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gordonii* Ralim. & Petra Hoffm.

Cicca goudotiana (Baillon 1861: 62) R.W.Bouman, *comb. nov.* Basionym: *Menarda goudotiana* Baill., homotypic synonym: *Phyllanthus goudotianus* (Baill.) Müll.Arg. (1863: 8).

Cicca humbertiana (Leandri 1938: 194) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus humbertianus* Leandri.

Cicca iratsiensis (Leandri 1938: 193) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus iratsiensis* Leandri.

Cicca isomonensis (Leandri 1957: 229) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus isomonensis* Leandri.

Cicca mananarensis (Leandri 1957: 230) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mananarensis* Leandr.

Cicca mantadiensis (Ralimanana & Hoffmann 2014: 280) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mantadiensis* Ralim. & Petra Hoffm.

Cicca multiflora (Poiret 1804: 229) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus multiflorus* Poir.

Cicca obdeltophylla (Leandri 1957: 232) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus obdeltophyllus* Leandri.

Cicca L. subgenus **Betsileani** (Jean F.Brunel) R.W.Bouman, *comb. nov.*

Phyllanthus L. subgenus *Macraea* (Wight) Jean F.Brunel subsection *Betsileani* Brunel (1987: 299).—*Phyllanthus* L. subgenus *Betsileani* (Jean F.Brunel) Ralimanana & Hoffmann (2011: 338).—Type: *Phyllanthus betsileanus* Leandri = *Cicca betsileana* (Leandri) R.W.Bouman.

Diagnostic features: Herbs or shrubs, monoecious or dioecious, branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* spirally arranged at basal nodes, becoming distichous in distal nodes. *Inflorescences* axillary, unisexual fascicles, found on all axes. *Staminate flowers*: sepals (5 or) 6; disc glands (5 or) 6, free; stamens 3, filaments free, anthers dehiscing longitudinally, connectives non-apiculate; pollen perisyncolporate, exine reticulate. *Pistillate flowers*: sepals (5 or) 6; disc entire and lobed; ovary 3-locular; styles absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or faintly longitudinally striate.

Distribution: Madagascar.

Included species and taxonomic changes (3 spp.):

Cicca bathiana (Leandri 1933: 371) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bathianus* Leandri.

Cicca betsileana (Leandri 1933: 372) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus betsileanus* Leandri.

Cicca philippioides (Leandri 1933: 373) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus philippioides* Leandri.

Cicca L. subgenus **Cicca**

Cicca L. subgenus *Cicca*: Literature and type as under the genus.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, sometimes specialized in vegetative and floriferous branchlets. *Brachyblasts* present or absent. *Cataphyllary stipules* triangular or spinescent, indurate, base not auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, sometimes on specialized branchlets. *Staminate flowers*: sepals 4–6; disc glands 4–6, sometimes absent; stamens 2–6, filaments free, basifixed or connate, anthers dehiscing longitudinally, vertically, connectives non-apiculate; pollen: exine reticulate. *Pistillate flowers:* sepals 4–6; disc entire or segmented; ovary 2–4-locular; styles absent; stigmas bifid. *Fruits* baccate or capsular. *Seeds* trigonous or rounded, sometimes with a cavity at hilum, smooth or with minute striae.

Distribution: Africa, mainland Asia and South America.

Notes—1. Subgenus *Cicca* is distributed in Africa and the Neotropics and has one of the more complicated taxonomic histories. Species of subgenus *Cicca* have been treated in various genera, including *Margaritaria*, *Emblica* and *Phyllanthus* subgenus *Kirganelia* (Webster 2001b). Kathriarachchi *et al.* (2006), showed it to be part of a clade distinct from other species of *Kirganelia*, but related to section *Chorisandra*. The African section *Omphacodopsis* is related to sections *Cicca* and *Chorisandra* (Supplementary Fig. 1). All of these sections are characterized by the

presence of (usually) leafless branches with the inflorescences (also called cauliflorous panicles: Webster 1957). They also all have staminate flowers with free stamens, but the number of stamens and sepals differ between sections. Inflorescences and baccate fruits are also found in *Kirganelia*, which complicates the distinction between these two groups, but these can differ considerably in size or locule number.

2. Three sections are included in this treatment: *Chorisandra*, *Cicca*, and *Omphacodopsis*.

Cicca L. subgenus **Cicca** section **Chorisandra** (Wight) R.W.Bouman, *comb. nov.*

Chorisandra Wight (1853: 12, pl. 1994), nom. illeg., non *Chorizandra* Brown (1810: 221).—*Phyllanthus* subgenus *Kirganelia* (A.Juss.) Kurz section *Chorisandra* (Wight) Müller (1863: 2, 6 as '*Chorizandra'*); (1866: 333); Pax & Hoffmann (1921: 22); (1931: 61); Webster (1957: 52); (1997: 216).—*Chorizonema* Brunel (1987: 256).—Type: *Chorisandra pinnata* Wight (= formerly *Phyllanthus pinnatus* (Wight) G.L.Webster) = *Cicca pinnata* (Wight) R.W.Bouman.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 4–6; disc glands 4–6; stamens 2 (*C. kidna* (Challen & Petra Hoffm.) R.W.Bouman) or 6, filaments free, basifixed or connate (*C. kidna*); anthers dehiscing longitudinally, vertically. *Pistillate flowers*: sepals 4 or 5 (*C. kidna*) or 6 (*C. pinnata* (Wight) R.W.Bouman & *C. orientalis* (Craib) R.W.Bouman); disc entire; ovary 2- or 3-locular; styles absent; stigmas usually 3, bifid. *Fruits* baccate. *Seeds* trigonous, with cavity at hilum, smooth.

Distribution: Africa, mainland Asia.

Note—Brunel (1987) raised section *Chorisandra* to generic level, but opted to use the name *Chorizonema*, since the generic name *Chorisandra* was previously used in Cyperaceae. Chantaranothai (2007) reported that *C. orientalis* has an entire disc in the staminate flower, although this needs to be corroborated.

Included species and taxonomic changes (4 spp.):

Cicca coluteoides (Baillon ex Müller 1866: 335) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus coluteoides* Baill. ex Müll.Arg.

Cicca kidna (Challen & Hoffmann 2011: 935) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kidna* Challen & Petra Hoffm.

Cicca orientalis (Craib 1914: 285) R.W.Bouman, *comb. nov.* Basionym: *Chorisandra orientalis* Craib, homotypic synonym: *Phyllanthus orientalis* (Craib) Airy Shaw (1971: 495).

Cicca pinnata (Wight 1853: 13) R.W.Bouman, *comb. nov.* Basionym: *Chorisandra pinnata* Wight, homotypic synonym: *Phyllanthus pinnatus* (Wight) Webster (1957: 52).

Cicca L. subgenus **Cicca** section **Cicca**

Cicca L. subgenus *Cicca* section *Cicca:* Literature and type as under the genus.

Phyllanthus L. section *Cicca* (L.) Müller subsection *Eucicca* Müller (1863: 50), nom. inval.; (1866: 413).—*Phyllanthus* subgenus *Kirganelia* (A.Juss.) Kurz section *Cicca* (L.) Webster subsection *Cheramella* Kuntze in Post & Kuntze(1904: 434).—Type: *Phyllanthus acidus* (L.) Skeels = *Cicca acida* (L.) Merr.

Aporosella Chodat (1905: 488).—*Phyllanthus* L. subgenus *Cicca* (L.) G.L.Webster section *Aporosella* (Chodat) Webster (1957: 72).—*Phyllanthus* subgenus *Kirganelia* (A.Juss.) Kurz section *Cicca* (L.) Webster subsection *Aporosella* (Chodat) Webster (2001b: 381).—Type: *Phyllanthus chacoensis* Morong = *Cicca chacoensis* (Morong) R.W.Bouman.

Diagnostic features: Trees, rarely shrubs, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, on separate branchlets without leaves. *Staminate flowers*: sepals 4–6; disc glands 4–6 or absent; stamens 3 or 4 (rarely 2 or 5), filaments free; anthers dehiscing more or less vertically; pollen 3-syncolporate, exine reticulate. *Pistillate flowers*: sepals 4; disc lobed or segmented; staminodes sometimes present; ovary 2–4-locular; styles absent or present, short; stigmas bifid. *Fruits* woody or drupaceous, indehiscent. *Seeds* trigonous, smooth.

Distribution: South America and one widely cultivated species of unknown origin.

Note—Two former subsections of *Phyllanthus* section *Cicca* are here placed in synonymy. These subsections were upheld by Webster (1957) to distinguish the type species from other species of section *Cicca*. The species of both subsections were previously only distinguished by their leaf shape and whether they were monoecious (subsection *Cheramella* Kuntze) or dioecious (subsection *Aporosella* (Chodat) G.L.Webster). Section *Omphacodopsis* (Jean F.Brunel) R.W.Bouman is closely related to section *Cicca* and species of both sections are characterized by specialized floriferous branchlets and staminate flowers with free stamens (some exceptions), but they differ in fruit morphology.

Included species and taxonomic changes (3 spp.):

Cicca acida (L.) Merrill (1917: 314); Basionym: *Averrhoa acida* Linnaeus (1753: 428), homotypic synonym: *Phyllanthus acidus* (L.) Skeels (1909: 17).

Cicca chacoensis (Morong *in* Morong & Britton 1892: 218) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chacoensis* Morong.

Cicca elsiae (Urban 1919: 405) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus elsiae* Urb.

Cicca L. subgenus **Cicca** (L.) G.L.Webster section **Omphacodopsis** (Jean F.Brunel) R.W.Bouman, *comb. nov*.

Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Omphacodopsis* Brunel (1987: 279).—Type: *Phyllanthus physocarpus* Müll. Arg. = *Cicca physocarpa* (Müll.Arg.) R.W.Bouman.

Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Polyanthi* Brunel (1987: 283).—Type: *Phyllanthus polyanthus* Pax = *Cicca polyantha* (Pax) R.W.Bouman.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, sometimes specialized in vegetative and floriferous branchlets. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, flowers solitary or in unisexual or bisexual fascicles. *Staminate flowers*: sepals 4 or 5; disc glands 4 or 5; stamens 4 or 5, filaments free, basifixed (or connate in *C. delpyana*), anthers dehiscing longitudinally, vertically, connectives non-apiculate. *Pistillate flowers*: sepals 4 or 5, rarely 6; disc entire; ovary 3- or 4-locular; styles absent; stigmas bifid. *Fruits* baccate, but corky. *Seeds* ovoid-trigonous, reniform or rounded, smooth or with minute striae.

Distribution: Africa.

Note—Section *Omphacodopsis* was found to be nested within section *Polyanthi* (Bouman *et al*. 2020; supplementary fig. 1). Sections *Omphacodopsis* and *Polyanthi* were originally distinguished based on differences in fruit (berry versus inflated capsule) and seed shape (reniform versus rounded). To prevent paraphyly of section *Polyanthi*, it is here subsumed in section *Omphacodopsis* on the basis of their similarity in habit, inflorescence structure and floral morphology.

Included species and taxonomic changes (6 spp.):

Cicca delpyana (Hutchinson 1913: 1047) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus delpyanus* Hutch.

Cicca engleri (Pax 1895: 236) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus engleri* Pax.

Cicca physocarpa (Müller 1864: 515) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus physocarpus* Müll.Arg.

Cicca polyantha (Pax 1899: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus polyanthus* Pax.

Cicca profusa (Brown *in* Stapf 1905: 113) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus profusus* N.E.Br.

Cicca schliebenii (Mansfeld ex Radcliffe-Smith 1981: 772) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus schliebenii* Mansf. ex Radcl.-Sm.

Cicca L. subgenus **Menarda** (Comm. ex A.Juss.) R.W.Bouman, *comb. nov*.

Menarda Comm. ex Jussieu (1824: 23, 109); Baillon (1858: 608); Baillon (1861: 46); Baillon (1862b: 231).—*Phyllanthus* L. section *Menarda* (Comm. ex A.Juss.) Müller (1863: 2, 7); (1866: 334); Pax & Hoffmann (1931: 62); Brunel (1987: 269).—*Phyllanthus* L. subgenus *Menarda* (Comm. ex A.Juss.) Ralimanana & Hoffmann (2014: 296).—Type: *Menarda cryptophila* Comm. ex A.Juss. (formerly *Phyllanthus cryptophilus* (Comm. ex A.Juss.) Müll.Arg.) = *Cicca cryptophila* (Comm. ex A.Juss.) R.W.Bouman.

Phyllanthus L. subgenus *Anisonemoides* (Jean F.Brunel) Ralimanana & Hoffmann section *Pseudogomphidium* Ralimanana & Cable (2020: 3).—Type: *Phyllanthus marojejiensis* (Leandri) Petra. Hoffm. & McPherson. = *Cicca marojejiensis* (Leandri) R.W.Bouman.

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform (to further ramified with leaves at base of ultimate branches), sometimes two opposite branches from same node. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* opposite, sometimes sub-opposite, or alternate. *Inflorescences* axillary, unisexual or bisexual fascicles, not on separate branchlets. *Staminate flowers*: sepals 5 (-6); disc glands 5, free, globose, reniform or absent; stamens 3–5, filaments free or fused, anthers dehiscing longitudinally, vertically, connectives (non-)apiculate; pollen 3- or 4-colporate, colpi diploporate, exine perforate to microreticulate. *Pistillate flowers*: sepals 5 (or 6); disc entire, lobed or reduced; ovary 3-locular, globose or depressed globose; styles present or absent; stigmas entire or bifid for up to 2/3 of the length. *Fruits* capsules. *Seeds* trigonous, smooth or thinly longitudinally striate.

Distribution: Madagascar.

Notes—1. Ralimanana & Hoffmann (2014) listed the wrong author of the name *Menarda*. This should remain de Jussieu, who first described it (de Jussieu 1824) as a separate genus, instead of Müller, who reduced it to a section (Müller 1863).

2. Baillon (1861b) strangely treats subgenus *Menarda* both as a separate genus (1861: 46), but also describes some species in *Phyllanthus* section *Menarda* (1862a: 62).

3. *Phyllanthus* subgenus *Anesonemoides* section *Pseudogomphidium* was created in the fourth part of the taxonomic revision of *Phyllanthus* in Madagascar (Ralimanana & Cable 2020). A new section was deemed necessary as the species that were originally placed in *Phyllanthus* subgenus *Gomphidium* (Ralimanana & Hoffmann 2011) were found to be closer to other species from Madagascar in the phylogenetic tree from Kawakita *et al.* (2009). However, if retained, this section would be paraphyletic as *Phyllanthus* subgenus *Menarda* was found to be the nested within this clade of species (Bouman *et al.* 2021; Supplementary Fig. 1).

Included species and taxonomic changes (13 spp.):

Cicca ankaratrae (Leandri 1957: 214) R.W.Bouman, *comb. nov.* Basionym: *Glochidion ankaratrae* Leandri, homotypic synonym: *Phyllanthus ankaratrae* (Leandri) Hoffmann & McPherson (2003: 308).

Cicca ankirindrensis (Ralimanana & Cable 2020: 3) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ankirindrensis* Ralim. & Cable.

Cicca bernieriana (Baillon ex Müller 1866: 361) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bernierianus* Baill. ex Müll.Arg.

Cicca coodei (Ralimanana & Hoffmann 2014: 298) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus coodei* Ralim. & Petra Hoffm.

Cicca cryptophila (Commerson ex de Jussieu 1824: 109) R.W.Bouman, *comb. nov.* Basionym: *Menarda cryptophila* Comm. ex A.Juss., homotypic synonym: *Phyllanthus cryptophilus* (Comm. ex A.Juss.) Müller (1863: 8).

Cicca humbertii (Leandri 1957: 215) R.W.Bouman, *comb. nov.* Basionym: *Glochidion humbertii* Leandri, homotypic synonym: *Phyllanthus humbertii* (Leandri) Hoffman & McPherson (2003: 308).

Cicca lichenisilvae (Leandri 1937: 29) R.W.Bouman, *comb. nov.* Basionym: *Glochidion lichenisilvae* Leandri, homotypic synonym: *Phyllanthus lichenisilvae* (Leandri) Hoffmann & McPherson (2003: 308).

Cicca marojejiensis (Leandri 1957: 215) R.W.Bouman, *comb. nov.* Basionym: *Glochidion marojejiense* Leandri, homotypic synonym: *Phyllanthus marojejiensis* (Leandri) Hoffmann & McPherson (2003: 308).

Cicca oreichtitus (Leandri 1934: 450) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus monticola* Leandri, nom. illeg., non *Phyllanthus monticola* Hutchinson & Dalziel (1928: 291), homotypic synonym: *Phyllanthus oreichtitus* Leandri (1935: 24).

Cicca perrieri (Leandri 1934: 606) R.W.Bouman, *comb. nov.* Basionym: *Glochidion perrieri* Leandri, homotypic synonym: *Phyllanthus perrieri* (Leandri) Hoffman & McPherson (2003: 308).

Cicca razakamalalae (Ralimanana & Cable 2020: 6) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus razakamalalae* Ralim. & Cable.

Cicca sambiranensis (Leandri 1934: 451) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sambiranensis* Leandri.

Cicca vakinankaratrae (Leandri 1957: 233) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vakinankaratrae* Leandri.

Dendrophyllanthus S.Moore

Dendrophyllanthus Moore (1921: 395).—Type: *Dendrophyllanthus comptonii* S.Moore (= formerly *Phyllanthus moorei* M.Schmid).

Phyllanthus L. section *Gomphidium* Baillon (1862b: 234); Müller (1866: 319); Schmid (1991: 64).—*Phyllanthus* L. section *Paragomphidium* Müller (1863: 3, 14), nom. superfl; (1866: 351).—*Glochidion* J.R.Forst. & G.Forst. section *Gomphidium* (Baill.) Müller (1863: 58, 70); Pax & Hoffmann (1931: 58).—*Phyllanthus* L. subgenus *Gomphidium* (Baill.) Webster (1967b: 338); (1971: 92).—Lectotype (selected by Webster 1967b): *Phyllanthus chamaecerasus* Baill. = *Dendrophyllanthus chamaecerasus* (Baill.) R.W.Bouman.

Diagnostic features: Herbs, shrubs or trees, monoecious, branching phyllanthoid, branchlets (bi)pinnatiform, glabrous or pubescent. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* distichous, sometimes opposite, branchlets sometimes with a single leaf. *Inflorescences* axillary, unisexual, rarely bisexual fascicles, sometimes paniculate but generally not on separate specialized branchlets. *Staminate flowers*: sepals 5 or 6, usually in two whorls, inner whorl often longer than androecium; disc entire or 3 or 6 massive glands or absent; stamens 3–20, filaments free or connate, anthers dehiscing vertically to obliquely to horizontally, connectives sometimes apiculate; pollen 3-colporate or 3-syncolporate, exine reticulate, vermiculate, pilate or ± vermiculate. *Pistillate flowers*: sepals 5 or 6, in two whorls, often differing in length, one whorl possibly accrescent or reduced to absent; disc entire, segmented or absent; ovary 3–5-locular; style present or absent; stigma tips entire or bifid. *Fruits* capsules. *Seeds* trigonous, smooth.

Distribution: Malesia, Australia and Pacific.

Included, but further unplaced species and taxonomic changes (1 sp.):

Dendrophyllanthus ciliaris (Baillon 1876: 373) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ciliaris* Baill.

Dendrophyllanthus S.Moore section **Dendrophyllanthus**

Dendrophyllanthus S.Moore section *Dendrophyllanthus*: Literature and type as under the genus.

Phyllanthus L. section *Phyllocalyx* Baillon (1862b: 236).—*Glochidion* J.R.Forst. & G.Forst. section *Physoglochidion* Müller (1863: 58, 71), *nom. superfl*.; Pax & Hoffmann (1931: 58).—*Phyllanthus* L. section *Physoglochidion* (Müll.Arg.) Müller (1866: 318), *nom. superfl*.—*Phyllanthus* L. subgenus *Gomphidium* (Baill.) G.L.Webster section *Gomphidium* Baill. subsection *Physoglochidion* (Müll.Arg.) Bouman in Bouman *et al.* (2018: 170).—Type: *Phyllanthus faguetii* Baill. = *Dendrophyllanthus faguetii* (Baill.) R.W.Bouman.

Leichhardtia Mueller (1876: 67), nom. illeg., non *Leichardtia* Brown (1849: 81).—*Phyllanthus* L. section *Leichhardtia* (F.Muell.) Diels (1931: 308).—Type: *Leichhardtia clamboides* F.Muell. (formerly *Phyllanthus clamboides* (F.Muell.) Diels) = *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman.

Nymania Schumann (1905: 291), nom. illeg., non *Nymania* Lindberg (1868: 290).—*Phyllanthus* L. subgenus *Gomphidium* (Baill.) G.L.Webster section *Nymania* (K.Schum.) Smith (1912: 781).—Type: *Nymania insignis* K.Schum (= formerly a synonym of *Phyllanthus schumannianus* L.S.Sm.) = *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman.

Hexaspermum Domin (1927: 869)).—Type: *Hexaspermum paniculatum* (Oliv.) Domin (= based on *Phyllanthus paniculatus* Oliv.; formerly synonyms of *Phyllanthus clamboides* (F.Muell.) Diels) = *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman.

Diagnostic features: Shrubs or trees, monoecious, branching phyllanthoid, branchlets (bi)pinnatiform, glabrous or pubescent. *Brachyblasts* absent. *Leaves* distichous, sometimes opposite. *Inflorescences* axillary, mostly unisexual, some bisexual fascicles, or panicles. *Staminate flowers:* sepals 6, in two whorls, inner whorl often longer than androecium; disc 3 massive (bilobed) glands (rarely 6); stamens 3, filaments free or connate, anthers dehiscing vertically to obliquely, connectives apiculate; pollen oblate, 3-colporate or 3-syncolporate, exine rugulose-reticulate, vermiculate, pilate or ± vermiculate. *Pistillate flowers:* sepals 6, in two whorls, often differing in length, one whorl sometimes accrescent or reduced to absent; disc entire, sometimes very small to absent; ovary 3-locular; styles present or absent; stigmas entire (rarely bifid). *Fruits* capsules. *Seeds* trigonous.

Distribution: Malesia, Australia and Pacific.

Notes—1. McPherson & Schmid (1991) grouped many other taxa together in their informal groups 6 and 7, which correspond to *Dendrophyllanthus* sections *Dendrophyllanthus* and *Leptonema* (Baill.) R.W.Bouman. Any previously defined subsections were not treated separately by McPherson & Schmid (1991) since they are morphologically very similar. *Phyllanthus* subsection *Physoglochidion* was represented by only one species in the phylogenetic study of Bouman *et al.* (2021), if retained it would necessitate the recognition of several other subsections. As this might result in a confusing classification with morphologically very similar subsections, we have opted to subsume subsection *Physoglochidion* within *Dendrophyllanthus* section *Dendrophyllanthus*.

2. *Phyllanthus* subgenus *Gomphidium* section *Nymania* (K.Schum) J.J.Sm. was found to be paraphyletic with the rest of *Phyllanthus* section *Gomphidium* nested within (Bouman *et al.* 2021). Both sections have the same number of stamens and disc glands, but differ slightly in the fusion of the filaments and some pollen characters (Airy Shaw 1980a). However, species with free and connate filaments occur in the previous classification of *Phyllanthus* section *Nymania* (e.g. *D. tenuirhachis* (J.J.Sm.) R.W.Bouman: free; and *D. cuscutiflorus* (S.Moore) R.W.Bouman: connate). Bipinnatiform branchlets also occur in both sections, resulting in almost no distinction between the groups and hence they are here combined.

3. Some species with six staminate disc glands from the Philippines were shown to belong to the genus *Emblica* (e.g., *E. rufuschaneyi* (Welzen, R.W.Bouman & Ent) R.W.Bouman; R.W.Bouman; Bouman *et al.* 2020), which casts some doubt on the placement of similar species, such as *D. rheophila* (Airy Shaw) R.W.Bouman; this requires further study.

Included species and taxonomic changes (88 spp.):

Dendrophyllanthus acinacifolius (Airy Shaw & Webster 1971: 95) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus acinacifolius* Airy Shaw & G.L.Webster.

Dendrophyllanthus actephilifolius (Smith 1917: 543) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus actephilifolius* J.J.Sm.

Dendrophyllanthus amicorus (Webster 1986: 100) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amicorum* G.L.Webster.

Dendrophyllanthus amieuensis (Guillaumin 1962: 242) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amieuensis* Guillaumin.

Dendrophyllanthus aphanostyla (Airy Shaw & Webster 1971: 106) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aphanostylus* Airy Shaw & G.L.Webster.

Dendrophyllanthus apiculatus (Merrill 1920: 540) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus apiculatus* Merr.

Dendrophyllanthus ardisianthus (Airy Shaw & Webster 1971: 94) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ardisianthus* Airy Shaw & G.L.Webster.

Dendrophyllanthus avanguiensis (Schmid 1991: 182) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus avanguiensis* M.Schmid.

Dendrophyllanthus balansanus (Guillaumin 1929: 4) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus balansanus* Guillaumin.

Dendrophyllanthus bourgeoisii (Baillon 1862b: 235) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bourgeoisii* Baill.

Dendrophyllanthus buxoides (Guillaumin 1929: 6) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus buxoides* Guillaumin.

Dendrophyllanthus calcicola (Schmid 1991: 118) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus calcicola* M.Schmid.

Dendrophyllanthus castus (Moore 1921: 401) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus castus* S.Moore.

Dendrophyllanthus caudatus (Müller 1866: 321) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caudatus* Müll.Arg.

Dendrophyllanthus chamaecerasus (Baillon 1862b: 235) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chamaecerasus* Baill.

Dendrophyllanthus clamboides (Mueller 1876: 68) R.W.Bouman, *comb. nov.* Basionym: *Leichhardtia clamboides* F.Muell., homotypic synonym: *Phyllanthus clamboides* (F.Muell.) Diels (1931: 309).

Dendrophyllanthus cordatulus (Robinson 1909: 76) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cordatulus* C.B.Rob.

Dendrophyllanthus cornutus (Baillon 1862b: 236) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cornutus* Baill.

Dendrophyllanthus comptonii Moore (1921: 395), non *Phyllanthus comptonii* Moore 1921: 398), homotypic synonym: *Phyllanthus moorei* Schmid (1991: 159).

Dendrophyllanthus cuscutiflorus (Moore 1905: 148) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cuscutiflorus* S.Moore.

Dendrophyllanthus dzumacensis (Schmid 1991: 105) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dzumacensis* M.Schmid.

Dendrophyllanthus effusus (Moore 1923: 45) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus effusus* S.Moore.

Dendrophyllanthus faguetii (Baillon 1862b: 237) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus faguetii* Baill.

Dendrophyllanthus finschii (Schumann 1887: 205) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus finschii* K.Schum.

Dendrophyllanthus flaviflorus (Schumann & Lauterbach 1900: 388) R.W.Bouman, *comb. nov.* Basionym: *Actephila flaviflora* K.Schum. & Lauterb., homotypic synonym: *Phyllanthus flaviflorus* (K.Schum. & Lauterb.) Airy Shaw (1969: 39).

Dendrophyllanthus frodinii (Airy Shaw 1972: 74) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus frodinii* Airy Shaw.

Dendrophyllanthus gjellerupi (Smith 1912: 780) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gjellerupi* J.J.Sm.

Dendrophyllanthus glochidioides (Elmer 1911: 1302) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus glochidioides* Elmer.

Dendrophyllanthus helenae (M.Schmid 1991: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus helenae* M.Schmid.

Dendrophyllanthus heterodoxus (Müller *in* de Candolle 1866: 321) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus heterodoxus* Müll. Arg.

Dendrophyllanthus houailouensis (Schmid 1991: 93) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus houailouensis* M.Schmid.

Dendrophyllanthus insulae-japen (Airy Shaw 1978: 37) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus insulae-japen* Airy Shaw.

Dendrophyllanthus jaffrei (Schmid 1991: 113) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus jaffrei* M.Schmid.

Dendrophyllanthus jaubertii (Vieillard ex Guillaumin 1929: 9) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus jaubertii* Vieill. ex Guillaumin.

Dendrophyllanthus koghiensis (Guillaumin 1929: 10) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus koghiensis* Guillaumin.

Dendrophyllanthus koniamboensis (Schmid 1991: 136) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus koniamboensis* M.Schmid.

Dendrophyllanthus kostermansii (Airy Shaw 1974: 296) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kostermansii* Airy Shaw.

Dendrophyllanthus kouaouaensis (Schmid 1991: 114) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kouaouaensis* M.Schmid.

Dendrophyllanthus koumacensis (Guillaumin 1965: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus koumacensis* Guillaumin.

Dendrophyllanthus macphersonii (Schmid 1991: 142) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus macphersonii* M.Schmid.

Dendrophyllanthus mangenotii (Schmid 1991: 156) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mangenotii* M.Schmid.

Dendrophyllanthus merinthopodus (Diels 1931: 310) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus merinthopodus* Diels.

Dendrophyllanthus montis-fontius (Schmid 1991: 78) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus montis-fontium* M.Schmid.

Dendrophyllanthus mouensis (Schmid 1991: 104) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mouensis* M.Schmid.

Dendrophyllanthus natoensis (Schmid 1991: 171) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus natoensis* M.Schmid.

Dendrophyllanthus ningaensis (Schmid 1991: 144) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ningaensis* M.Schmid.

Dendrophyllanthus nothisii (Schmid 1991: 179) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nothisii* M.Schmid.

Dendrophyllanthus ovatifolius (Smith 1920: 390) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ovatifolius* J.J.Sm.

Dendrophyllanthus pancherianus (Baillon 1862b: 235) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pancherianus* Baill.

Dendrophyllanthus papuanus (Gage 1917: 479) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus papuanus* Gage.

Dendrophyllanthus paucitepalus (Schmid 1991: 140) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus paucitepalus* M.Schmid.

Dendrophyllanthus pergracilis (Gillespie 1932: 18) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pergracilis* Gillespie.

Dendrophyllanthus petchikaraensis (Schmid 1991: 90) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus petchikaraensis* M.Schmid.

Dendrophyllanthus pilifer (Schmid 1991: 120) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pilifer* M.Schmid.

Dendrophyllanthus pindaiensis (Schmid 1991: 183) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pindaiensis* M.Schmid.

Dendrophyllanthus pinjenensis (Schmid 1991: 92) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pinjenensis* M.Schmid.

Dendrophyllanthus platycalyx (Müller *in* de Candolle 1866: 318) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus platycalyx* Müll. Arg.

Dendrophyllanthus poliborealis (Airy Shaw 1978: 36.) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poliborealis* Airy Shaw.

Dendrophyllanthus polygynus (Schmid 1991: 97) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus polygynus* M.Schmid.

Dendrophyllanthus poueboensis (Schmid 1991: 154) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poueboensis* M.Schmid.

Dendrophyllanthus poumensis (Guillaumin 1929: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poumensis* Guillaumin.

Dendrophyllanthus praelongipes (Airy Shaw & Webster 1971: 100) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus praelongipes* Airy Shaw & G.L.Webster.

Dendrophyllanthus pterocladus (Moore 1921: 400) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pterocladus* S.Moore.

Dendrophyllanthus pulchellus (Airy Shaw 1969: 22) R.W.Bouman, *comb. nov.* Basionym *Glochidion pulchellum* Airy Shaw, homotypic synonym: *Phyllanthus stultitiae* Airy Shaw (1978: 368).

Dendrophyllanthus pullenii (Airy Shaw & Webster 1971: 105) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pullenii* Airy Shaw & G.L.Webster.

Dendrophyllanthus quintuplinervis (Schmid 1991: 148) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus quintuplinervis* M.Schmid.

Dendrophyllanthus rheophilus (Airy Shaw 1966: 385) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rheophilus* Airy Shaw.

Dendrophyllanthus rosselensis (Airy Shaw & Webster 1971: 103) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rosselensis* Airy Shaw & G.L.Webster.

Dendrophyllanthus rubriflorus (Smith 1912: 781) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rubriflorus* J.J.Sm.

Dendrophyllanthus rupiinsularis (Hosokawa 1935: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rupiinsularis* Hosok.

Dendrophyllanthus salomonis (Airy Shaw 1978: 368) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus salomonis* Airy Shaw.

Dendrophyllanthus securinegoides (Merrill 1914: 490) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus securinegoides* Merr.

Dendrophyllanthus smithianus (Webster 1986: 99) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus smithianus* G.L.Webster.

Dendrophyllanthus stenophyllus (Guillaumin 1929: 17) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus stenophyllus* Guillaumin.

Dendrophyllanthus stipitatus (Schmid 1991: 178) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus stipitatus* M.Schmid.

Dendrophyllanthus tabularis (Airy Shaw 1980b: 598) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tabularis* Airy Shaw.

Dendrophyllanthus tagulae (Airy Shaw & Webster 1971: 102) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tagulae* Airy Shaw & G.L.Webster.

Dendrophyllanthus tangoensis (Schmid 1991: 162) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tangoensis* M.Schmid.

Dendrophyllanthus tenuipedicellatus (Schmid 1991: 98) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuipedicellatus* M.Schmid.

Dendrophyllanthus tenuirhachis (Smith 1908: t. 263) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuirhachis* J.J.Sm.

Dendrophyllanthus tiebaghiensis (Schmid 1991: 94) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tiebaghiensis* M.Schmid.

Dendrophyllanthus unioensis (Schmid 1991: 139) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus unioensis* M.Schmid.

Dendrophyllanthus utricularis (Airy Shaw & Webster 1971: 101) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus utricularis* Airy Shaw & G.L.Webster.

Dendrophyllanthus veillonii (Schmid 1991: 130) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus veillonii* M.Schmid.

Dendrophyllanthus vieillardii (Müller 1863: 70) R.W.Bouman, *comb. nov.* Basionym: *Glochidion vieillardii* Müll.Arg. (non *Phyllanthus vieillardii* Baillon 1862b: 236), homotypic synonym: *Phyllanthus tritepalus* Schmid (1991: 153).

Dendrophyllanthus virgultiramus (Däniker 1931: 169) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus virgultiramus* Däniker.

Dendrophyllanthus warburgii (Schumann 1905: 286) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus columnaris* Warburg (1891: 356), nom. illeg., non *Phyllanthus columnaris* Müller (1863: 15), homotypic synonym: *Phyllanthus warburgii* K.Schum.

Dendrophyllanthus wilkesianus (Müller 1866: 396) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus wilkesianus* Müll.Arg.

Dendrophyllanthus L. section **Leptonema** (Baill.) R.W.Bouman, *comb. nov.*

Phyllanthus L. section *Leptonema* Baillon (1862b: 234).—*Glochidion* J.R.Forst. & G.Forst. section *Pentaglochidion* Müller (1863: 58, 59), nom. superfl.; Pax & Hoffmann (1931: 58).—*Phyllanthus* L. section *Pentaglochidion* (Müll.Arg.) Müller (1866: 315), nom. superfl.—*Phyllanthus* L. (informal) groupe 6: Schmid (1991: 184).—Type: *Phyllanthus kanalensis* Baill. = *Dendrophyllanthus kanalensis* (Baill.) R.W.Bouman.

Glochidion J.R.Forst. & G.Forst. section *Adenoglochidion* Müller (1863: 58); Pax & Hoffmann (1931: 58).—*Phyllanthus* L. section

Adenoglochidion (Müll.Arg.) Müller (1866: 319).—Type: *Phyllanthus aeneus* Baill. = *Dendrophyllanthus aeneus* (Baill.) R.W.Bouman.

Phyllanthus L. section *Polyandroglochidion* Moore (1921: 402); Pax & Hoffmann (1931: 61).—Type: *Phyllanthus sylvincola* S.Moore = *Dendrophyllanthus sylvincolus* (S.Moore) R.W.Bouman.

Phyllanthus L. section *Meiandroglochidion* Moore (1921: 402); Pax & Hoffmann (1931: 61).—Type: *Phyllanthus ligustrifolius* S.Moore = *Dendrophyllanthus ligustrifolius* (S.Moore) R.W.Bouman.

Phyllanthus L. section *Eleutherogynium* Müller (1863: 4, 14).—*Glochidion* J.R.Forst. & G.Forst. section *Eleutherogynium* (Müll.Arg.) Pax & Hoffmann (1931: 58).—*Phyllanthus* L. subgenus *Gomphidium* (Baill.) G.L.Webster section *Adenoglochidion* (Müll.Arg.) Müll. Arg. subsection *Eleutherogynium* (Müll.Arg.) Webster ex Bouman *in* Bouman *et al.* (2018: 170).—Type: *Phyllanthus loranthoides* Baill. = *Dendrophyllanthus loranthoides* (Baill.) R.W.Bouman.

Glochidion J.R.Forst. & G.Forst. section *Chorizogynium* Müller (1863: 58).—Lectotype (designated by Webster 1986): *Phyllanthus macrochorion* Baill. = *Dendrophyllanthus macrochorion* (Baill.) R.W.Bouman.

Phyllanthus L. section *Heteroglochidion* Müller (1866: 319).—*Glochidion* J.R.Forst. & G.Forst. section *Heteroglochidion* (Müll.Arg.) Pax & Hoffmann (1931: 58).—Type: *Phyllanthus baladensis* Baill. = *Dendrophyllanthus baladensis* (Baill.) R.W.Bouman.

Phyllanthus L. section *Scleroglochidion* Müller (1866: 317).—*Glochidion* J.R.Forst. & G.Forst. section *Scleroglochidion* (Müll.Arg) Pax & Hoffmann (1931: 62).—Type: *Phyllanthus myrianthus* Müll.Arg. = *Dendrophyllanthus myrianthus* (Müll.Arg.) R.W.Bouman.

Diagnostic features: Herbs, shrubs to trees, monoecious, branching phyllanthoid, branchlets pinnatiform, glabrous. *Brachyblasts* absent. *Leaves* distichous, sometimes branchlets bearing only a single leaf. *Inflorescences* axillary, often bisexual fascicles. *Staminate flowers*: sepals 5, sometimes 6, not clearly biseriate; disc entire or free glands, sometimes absent; stamens 3 or 5(7—20), filaments free, inserted often on a large receptacle, anthers dehiscing vertically to horizontally, often oblique, connectives non-apiculate; pollen 3-syncolporate, exine reticulate. *Pistillate flowers:* sepals 5 or 6; disc entire or segmented, sometimes absent; ovary 3- to 5-locular; styles absent or present; stigmas entire, rarely bifid (*D. nitens* (M.Schmid) R.W.Bouman, *D. torrentium* (Müll.Arg.) R.W.Bouman). *Fruits* capsules. *Seeds* trigonous.

Distribution: Malesia, Australia and Pacific (mainly New Caledonia).

Notes—1. *Phyllanthus* section *Leptonema* is nested within a paraphyletic *Phyllanthus* section *Adenoglochidion* (Bouman *et al.* 2021) and the two groups are therefore combined and transferred as *Dendrophyllanthus* section *Leptonema*. Section *Leptonema* was originally distinguished from other groups based on its absent disc and the 5-locular ovary in the pistillate flower (Baillon 1862b). However, several species within former *Phyllanthus* section *Adenoglochidion* (specifically the former subsection *Eleutherogynium*) have a reduced or an absent disc, so the combination of these two sections is not surprising. The number of locules is variable within *Dendrophyllanthus* and also in the genus *Glochidion* and is probably related to a pollination mutualism with moths as the pollinator.

2. McPherson & Schmid (1991) adopted a broad delimitation of *Phyllanthus* section *Adenoglochidion*, which is here subsumed within section *Leptonema*. This means that sections *Polyandroglochidion* S.Moore and *Meiandroglochidion* S.Moore are also subsumed, which only alters the description in relation to the number of stamens, with the other characters, including those from pistillate flowers, overlapping. *Polyandroglochidion* was defined on the basis of its absent discs glands, the 14 free stamens, 3- or 4-locular ovary and 3 or 4 free undivided stigmas. *Phyllanthus* section *Meiandroglochidion* was defined as close to *Phyllanthus* section *Polyandroglochidion*, but differing in the presence of a disc in the staminate flowers and with fewer stamens (7–10).

Included species and taxonomic changes (72 spp.):

Dendrophyllanthus aeneus (Baillon 1862b: 231) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aeneus* Baill.

Dendrophyllanthus aoupinieensis Schmid 1991: 275) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aoupinieensis* M.Schmid.

Dendrophyllanthus artensis (Schmid 1991: 242) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus artensis* M.Schmid.

Dendrophyllanthus baladensis (Baillon 1862b: 233) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baladensis* Baill.

Dendrophyllanthus baraouaensis (Schmid 1991: 272) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baraouaensis* M.Schmid.

Dendrophyllanthus boguenensis (Schmid 1991: 286) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus boguenensis* M.Schmid.

Dendrophyllanthus bupleuroides (Baillon 1862b) 233) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bupleuroides* Baill.

Dendrophyllanthus brassii (White 1936: 81) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus brassii* C.T.White.

Dendrophyllanthus casearioides (Moore 1921: 397) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus casearioides* S.Moore.

Dendrophyllanthus caesius (Airy Shaw & Webster 1971: 90) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caesius* Airy Shaw & G.L.Webster.

Dendrophyllanthus carlottae (Schmid 1991: 258) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carlottae* M.Schmid.

Dendrophyllanthus caudatifolius (Merrill 1926: 403) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caudatifolius* Merr.

Dendrophyllanthus cherrieri (Schmid 1991: 278) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cherrieri* M.Schmid.

Dendrophyllanthus chrysofructa Strijk & R.W.Bouman, *nom. nov*. Basionym: *Phyllanthus valeriae* Schmid (1991: 217), nom. illeg., non *Phyllanthus valerii* Standley (1937: 619).

Dendrophyllanthus conjugatus (Schmid 1991: 279) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus conjugatus* M.Schmid.

Dendrophyllanthus dracunculoides (Baillon 1862b: 239) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dracunculoides* Baill.

Dendrophyllanthus deciduiramus (Däniker 1931: 167) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus deciduiramus* Däniker.

Dendrophyllanthus dorotheae (Schmid 1991: 300) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dorotheae* M.Schmid.

Dendrophyllanthus dumbeaensis (Schmid 1991: 200) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dumbeaensis* M.Schmid.

Dendrophyllanthus erwinii (Hunter & Bruhl 1996: 130) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus erwinii* J.T.Hunter & J.J.Bruhl.

Dendrophyllanthus favieri (Schmid 1991: 262) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus favieri* M.Schmid.

Dendrophyllanthus fimbriatitepalus (Guillaumin 1937: 300) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fimbriatitepalus* Guillaumin.

Dendrophyllanthus fractiflexus (Schmid 1991: 238) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fractiflexus* M.Schmid.

Dendrophyllanthus francii (Guillaumin 1927: 273) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus francii* Guillaumin.

Dendrophyllanthus gneissicus (Moore 1921: 399) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus* gneissicus S.Moore.

Dendrophyllanthus golonensis (Schmid 1991: 304) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus golonensis* M.Schmid.

Dendrophyllanthus guillauminii (Däniker 1931: 167) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus guillauminii* Däniker.

Dendrophyllanthus hypospodius (Mueller 1892: 177) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hypospodius* F.Muell.

Dendrophyllanthus kanalensis (Baillon 1862b: 234) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kanalensis* Baill.

Dendrophyllanthus lacerosus (Airy Shaw 1980c: 386) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lacerosus* Airy Shaw.

Dendrophyllanthus lacunarius (Mueller 1855: 14) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lacunarius* F.Muell.

Dendrophyllanthus lacunellus (Airy Shaw 1980c: 387) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lacunellus* Airy Shaw.

Dendrophyllanthus ligustrifolius (Moore 1921: 402) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ligustrifolius* S.Moore.

Dendrophyllanthus longiramosus (Guillaumin 1962: 292, as '*longeramosa*') R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus longiramosus* Guillaumin.

Dendrophyllanthus loranthoides (Baillon 1862b: 238) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus loranthoides* Baill.

Dendrophyllanthus luciliae (Schmid 1991: 269) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus luciliae* M.Schmid.

Dendrophyllanthus macrochorion (Baillon 1862b: 232) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus macrochorion* Baill.

Dendrophyllanthus mandjeliaensis (Schmid 1991: 315) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mandjeliaensis* M.Schmid.

Dendrophyllanthus margaretae (Schmid 1991: 316) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus margaretae* M.Schmid.

Dendrophyllanthus maritimus (Smith 1912: 779) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus maritimus* J.J.Sm.

Dendrophyllanthus memaoyaensis (Schmid 1991: 274) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus memaoyaensis* M.Schmid.

Dendrophyllanthus meuieensis (Schmid 1991: 249) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus meuieensis* M.Schmid.

Dendrophyllanthus montrouzieri (Guillaumin 1913: 109) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus montrouzieri* Guillaumin.

Dendrophyllanthus mooreanus R.W.Bouman, *nom. nov*. Basionym: *Phyllanthus comptonii* S.Moore (1921: 398) (non *Dendrophyllanthus comptonii* S.Moore 1921: 395).

Dendrophyllanthus moratii (Schmid 1991: 313) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus moratii* M.Schmid.

Dendrophyllanthus myrianthus (Müller 1866: 317) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus myrianthus* Müll.Arg.

Dendrophyllanthus nitens (Schmid 1991: 239) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nitens* M.Schmid.

Dendrophyllanthus ouveanus (Däniker 1931: 168) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ouveanus* Däniker.

Dendrophyllanthus parainduratus (Schmid 1991: 228) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus parainduratus* M.Schmid.

Dendrophyllanthus parangoyensis (Schmid 1991: 250) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus parangoyensis* M.Schmid.

Dendrophyllanthus peltatus (Guillaumin 1929: 13) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus peltatus* Guillaumin.

Dendrophyllanthus pronyensis (Guillaumin 1927: 273) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pronyensis* Guillaumin.

Dendrophyllanthus pseudotrichopodus (Schmid 1991: 245) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pseudotrichopodus* M.Schmid.

Dendrophyllanthus ramosii (Quisumbing & Merrill 1928: 160) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ramosii* Quisumb. & Merr.

Dendrophyllanthus rhodocladus (Moore 1921: 397) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rhodocladus* S.Moore.

Dendrophyllanthus rozennae (Schmid 1991: 303) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rozennae* M.Schmid.

Dendrophyllanthus salicifolius (Baillon 1862b: 239) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus salicifolius* Baill.

Dendrophyllanthus sarasinii (Guillaumin 1929: 16) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sarasinii* Guillaumin.

Dendrophyllanthus sauropodoides (Airy Shaw 1980c: 216) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sauropodoides* Airy Shaw.

Dendrophyllanthus serpentinus (Moore 1921: 399) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus serpentinus* S.Moore.

Dendrophyllanthus sylvincola (Moore 1921: 401) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sylvincola* S.Moore.

Dendrophyllanthus tireliae (Schmid 1991: 246) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tireliae* M.Schmid.

Dendrophyllanthus tixieri (Schmid 1991: 241) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tixieri* M.Schmid.

Dendrophyllanthus torrentium (Müller 1866: 316) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus torrentium* Müll.Arg.

Dendrophyllanthus trichopodus (Guillaumin 1929: 17) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus trichopodus* Guillaumin, Arch. Bot. Mém. 2(3: (.

Dendrophyllanthus umbricolus (Guillaumin 1929: 18) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus umbricola* Guillaumin.

Dendrophyllanthus unifoliatus (Schmid 1991: 198) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus unifoliatus* M.Schmid.

Dendrophyllanthus verrucicaulis (Airy Shaw 1978: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus verrucicaulis* Airy Shaw.

Dendrophyllanthus vespertilio (Baillon 1862b: 233) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vespertilio* Baill.

Dendrophyllanthus vulcani (Guillaumin 1962: 248) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vulcani* Guillaumin.

Dendrophyllanthus yaouhensis (Schlechter 1906: 146) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus yaouhensis* Schltr.

Dendrophyllanthus yvettae (Schmid 1991: 309) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus yvettae* M.Schmid.

Clade G—Figs. 1, 2L & M (supplementary fig. 1)

Emblica Gaertn.

Emblica Gaertner (1790: 122); de Jussieu (1824: 20); Wight (1852: t. 1896); Ridley (1924: 217); Das (1940: 159).—*Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz (1873: 238); Webster (1967a: 194).—*Phyllanthus* L. section *Emblica* (Gaertn.) Baillon (1858: 626); Müller (1863: 3, 14); (1866: 351); Hooker (1887: 286); Boerlage (1900: 212); Pax & Hoffmann (1931: 64); Webster (1997: 219).—Type: *Emblica officinalis* Gaertn. (= formerly *Phyllanthus emblica* L.).

Dichelactina Hance *in* Walpers (1852: 375).—Type: *Dichelactina nodicaulis* Hance = *Emblica officinalis* Gaertn.

Phyllanthus L. section *Typhophyllanthus* Kuntze subsection *Urinaria* Kuntze *in* Post & Kuntze (1904: 434).—*Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz section *Urinaria* (Kuntze) Webster (1955: 51); (1957: 192); (1970: 65); (1997: 227); Schmid (1991: 54); Ralimanana & Hoffmann *in* Ralimanana *et al.* (2013: 555).—*Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz section *Urinaria* G.L.Webster subsection *Urinaria* (Kuntze) Haicour & Rossignol *in* Rossignol *et al.* (1987: 1857).—Type: *Phyllanthus urinaria* L. = *Emblica urinaria* (L.) R.W.Bouman.

Phyllanthus L. subgenus *Emblica* (Gaertn.) Kurz section *Emblica* (Gaertn.) Baill. subsection *Baeobotryoides* Brunel (1987: 232).—Type: *Phyllanthus baeobotryoides* Wall. ex Müll.Arg. = *Emblica baeobtoryoida* (Wall. ex Müll.Arg.) R.W.Bouman.

Diagnostic features: Herbs, shrubs or trees, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* sometimes present. *Cataphyllary stipules* ovate-triangular, membranous or indurate, base (not) auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, sometimes paniculate. *Staminate flowers:* sepals 6; disc glands 6, alternating with sepals; stamens 3, filaments connate, anthers elongate, dehiscing vertically, connectives sometimes apiculate; pollen prolate to spheroidal, 4- or 5-colporate or 5-brevisulcate, colpi monoporate, exine reticulate; pistillode absent. *Pistillate flowers:* sepals 6; disc entire; ovary 3-locular, sometimes tuberculate in herbaceous species; styles present; stigmas bifid. *Fruits* capsules or drupes. *Seeds* trigonous, smooth or with transverse ridges.

Distribution: Mainland Asia, Malesia, Australia and one pantropical invasive (*E. urinaria*).

Notes—1. *Phyllanthus* subgenus *Emblica* was considered to have a disjunct distribution with four included sections, two from the Neotropics (*Microglochidion* and *Pityrocladus*) and two from the Palaeotropics (*Urinaria* and *Emblica*) (Webster 2002). In Bouman *et al.* (2021) it was shown that *Phyllanthus* subgenus *Emblica* was polyphyletic. The genus *Emblica* is here separated as a strictly Palaeotropical genus and the Neotropical sections are retained within *Phyllanthus* (as subgenus *Microglochidion* and subgenus *Phyllanthus* section *Pityrocladus*).

2. The genus *Emblica* is sister to a clade that contains the genera *Glochidion* (including *Phyllanthodendron* (Hemsl.) R.W.Bouman), *Breynia* (including *Sauropus*) and *Synsostemon*. The androecium may be similar to those found in the species of *Glochidion* subgenus *Phyllanthodendron*, but species in the groups differ in the shape of the disc glands in both types of flowers (ligulate glands in both flower types in subgenus *Phyllanthodendron*).

3. Staminate flowers within this genus are quite typical and usually have six sepals, six free orbicular disc glands

and three stamens with connate filaments and vertically dehiscing anthers. However, some treatments are contradicting with six reported stamens, although this possibly refers to thecae (Chantaranothai 2007) or an entire disc (Chakrabarty & Balakrishnan 2018). These characters need to be verified as they contradict earlier descriptions (Hooker 1887; Beille 1927) without explanation. These characters have been tentatively included in the provided keys, but not in the above description.

4. We retain no further subdivision within the genus *Emblica* as the diagnostic characters of previously defined sections and subsections are minor. *Phyllanthus* section *Emblica* and section *Urinaria* differed mostly in habit (shrubs and trees vs. herbs), although woody shrubby plants from the Philippines were also placed in section *Urinaria*. *Emblica rufuschaneyi*, a shrubby species that would be placed in section *Emblica* is sister to a clade of herbaceous species and would result in a morphologically heterogeneous group if included. The staminate flowers in *Phyllanthus* sections *Emblica* and *Urinaria* are similar and we therefore opted to not retain any of the infrageneric groups. *Phyllanthus* subsection *Baeobotryoides*, which was created by Brunel (1987) to accommodate species with specialized inflorescence stalks, is also subsumed to avoid paraphyly. The genus has not been revised recently and species treatments have been scattered across several other sections in older classifications of the genus *Phyllanthus*.

5. Rossignol *et al.* (1987) conducted a very thorough study of *E. urinaria* and several related species including morphology, Karyology and cross-breeding barriers. This resulted in a systematic revision which aimed to divide *Phyllanthus* section *Urinaria* into three subsections (subsection *Urinaria*, subsection *Arenarius* and subsection *Benguetensis*), but they only provided a full description for subsection *Urinaria*. Another of these subsections was planned to be published by Webster (2002 manuscript synopsis of subgenus *Phyllanthus*). Since these subsections delimit only a few species with very limited characters, these will not be pursued further.

6. Webster (1955) used the name of section *Urinaria*, based on the pre-Linnean work by Hermann (1717) and Burman (1737), but the name was validly published before as a subsection by Kuntze (1904) and placed in his section *Typhophyllanthus*. Therefore, the original author becomes Kuntze and not Webster as listed in Ralimanana & Hoffmann (2011) and Bouman *et al.* (2018).

Included species and taxonomic changes (45 spp.):

Emblica albizzioides (Kurz 1873: 239) R.W.Bouman, *comb. nov.* Basionym: *Cicca albizzioides* Kurz, homotypic synonym: *Phyllanthus albizzioides* (Kurz) Hooker (1887: 289).

Emblica anamalayanus (Gamble 1925: 330) R.W.Bouman, *comb. nov.* Basionym: *Pseudoglochidion anamalayanum* Gamble, homotypic synonym: *Phyllanthus anamalayanus* (Gamble) Webster (1994: 45).

Emblica andamanicus (Balakrisnan & Nair 1982 publ. 1983: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus andamanicus* N.P.Balakr. & N.G.Nair. (non *Phyllanthus andamanicus* Kurz (1870: 47) pro syn. = *Glochidion helferi* (Müler 1865a: 372) Hook.f. (1887: 311)), homotypic synonym: *Phyllanthus balakrishnairii* Govaerts & Radcliffe-Smith (1996: 176).

Emblica angkorensis (Beille 1927: 583) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus angkorensis* Beille.

Emblica arenarius (Beille 1927: 587) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus arenarius* Beille.

Emblica baeobotryoides (Wallich ex Müller 1863: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baeobotryoides* Wall. ex Müll. Arg.

Emblica benguetensis (Robinson 1909: 78) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus benguetensis* C.B.Rob.

Emblica bokorensis (Tagane 2015: 126) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bokorensis* Tagane.

Emblica chamaepeuce (Ridley 1893: 345) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chamaepeuce* Ridl.

Emblica chayamaritiae (Chantaranothai & Kantachot *in* Kantachot & Chantaranothai 2013: 217) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chayamaritiae* Chantar. & Kantachot.

Emblica coi (Wu, Ferreras & Chen 2017: 375) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus coi* M.J.Wu, Ferreras & Y.J.Chen.

Emblica collinsiae (Craib 1913: 72) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus collinsiae* Craib.

Emblica columnaris (Müller 1863: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus columnaris* Müll.Arg. (non *Phyllanthus columnaris* Warburg 1891: 356, nom. illeg.).

Emblica dealbatus (Alston 1931: 257) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dealbatus* Alston.

Emblica embergeri (Haicour & Rossignol *in* Rossignol *et al.* 1987: 1860) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus embergeri* Haicour & Rossignol.

Emblica erythrotrichus (Robinson 1911: 333) R.W.Bouman, comb. nov. Basionym: Phyllanthus erythrotrichus C.B.Rob.

Emblica geoffrayi (Beille 1927: 584) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus geoffrayi* Beille.

Emblica harmandii (Beille 1927: 586) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus harmandii* Beille.

Emblica multiflora (Hasskarl 1844: 240) R.W.Bouman, *comb. nov.* Basionym: *Agyneia multiflora* Hassk. (non *Phyllanthus multiflorus* Poiret (1804: 299), homotypic synonym: *Phyllanthus hasskarlianus* Müller (1863: 16).

Emblica fischeri Gamble (1925: 330) (non *Phyllanthus fischeri* Pax 1894: 77), homotypic synonym: *Phyllanthus indofischeri* Bennet *in* Raizada & Bennet (1983: 221).

Emblica kerrii (Airy Shaw 1969: 32) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kerrii* Airy Shaw.

Emblica lawii (Graham 1839: 181) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lawii* J.Graham.

Emblica marianus (Müller 1863: 17) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus marianus* Müll.Arg.

Emblica niinamii (Hayata 1904: 14) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus niinamii* Hayata.

Emblica officinalis Gaertner (1791: 122), homotypic synonym: *Phyllanthus emblica* Linnaeus (1753: 982), homotypic synonym: *Cicca emblica* (L.) Kurz (1877: 352).

Emblica oxyphyllus (Miquel 1861: 448) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus oxyphyllus* Miq. (non *Phyllanthus oxyphyllus* Müller, 1863: 40, nom. illeg.).

Emblica pachyphyllus (Müller 1866: 353) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pachyphyllus* Müll.Arg.

Emblica pacoensis (Thin 1992: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pacoensis* Thin.

Emblica pectinata (Hooker 1887: 290) Ridley (1924: 217), Basionym: *Phyllanthus pectinatus* Hook.f.

Emblica petelotii (Croizat 1942a: 30) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus petelotii* Croizat.

Emblica phuquocensis (Beille 1927: 581) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus phuquocensis* Beille.

Emblica prainianus (Collett & Hemsley 1890: 123) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus prainianus* Collett & Hemsl.

Emblica racemosa (Linnaeus f. 1782: 415) Sprengel (1826: 29), Basionym: *Phyllanthus racemosus* L.f., homotypic synonym: *Phyllanthus polyphyllus* Willdenow (1805: 586).

Emblica rheophyticus (Gilbert & Li 2008: 188) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rheophyticus* M.G.Gilbert & P.T.Li.

Emblica rufuschaneyi (van Welzen, Bouman & van der Ent *in* Bouman *et al.* 2018a: 4) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rufuschaneyi* Welzen, R.W.Bouman & Ent.

Emblica rupicola (Elmer 1910: 927) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rupicola* Elmer.

Emblica saffordii (Merrill 1914: 104) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus saffordii* Merr.

Emblica scabrifolius (Hooker 1887: 299) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus scabrifolius* Hook.f.

Emblica societatis (Müller 1866: 364) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus societatis* Müll.Arg.

Emblica submarginalis (Airy Shaw 1982: 33) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus submarginalis* Airy Shaw.

Emblica sulcatus (Hunter & Bruhl 1997b: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sulcatus* J.T.Hunter & J.J.Bruhl.

Emblica thaii (Thin 1992: 22) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus thaii* Thin.

Emblica trungii (Thin 1992: 22) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus trungii* Thin.

Emblica tsarongensis (Smith 1921: 177) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tsarongensis* W.W.Sm.

Emblica urinaria (Linnaeus 1753: 982) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus urinaria* L.

Clade H—Figs. 1, 2P, Q & R (Supplementary Fig. 1)

Glochidion J.R.Forst. & G.Forst.

Glochidion Forster & Forster (1776: t.57), nom. cons; Hooker (1887: 305); Beille (1927: 608); Airy Shaw (1972: 271); Whitmore (1973: 98); Webster (1994: 46); van Welzen (2000: 56); van Welzen *in* van Welzen *et al.* (2000: 81); Radcliffe-Smith (2001: 47); van Welzen (2007: 308); Webster (2014: 79).—Type: *Glochidion ramiflorum* J.R.Forst & G.Forst.

Agyneia Linnaeus (1771: 161); Baillon (1858: 630).—Lectotype (designated by Webster 1994): *Agyneia pubera* L. = *Glochidion puberum* (L.) Müll.Arg.

Bradleia Banks ex Gaertner (1790: 127).—Type: *Bradleia sinica* Gaertn. = *Glochidion sinicum* (Gaertn.) Hook. & Arn.

Gynoon de Jussieu (1823: 335); (1824: 17).—Type: *Gynoon rigidum* A.Juss. = *Glochidion rigidum* (A.Juss.) Müll.Arg.

Glochidionopsis Blume (1826: 588); Baillon (1858: 639).—Type: *Glochidionopsis sericea* Blume = *Glochidion sericeum* (Blume) Hook. f.

Glochisandra Wight (1852: 26).—Type: *Glochisandra acuminata* Wight = *Glochidion lanceolarium* (Roxb.) Voigt.

Zarcoa Llanos (1857: 423).—Type: *Zarcoa philippica* Llanos = *Glochidion album* (Blanco) Boerl.

Glochidion J.R.Forst. & G.Forst. section *Hemiglochidion* Müller (1863: 58 61).—*Hemiglochidion* (Müll.Arg.) Schumann (1905: 289).—Lectotype (designated by Wheeler 1975): *Glochidion ramiflorum* J.R.Forst & G.Forst.

Phyllanthodendron Hemsley (1898: t. 2563, 2564).—*Phyllanthus* subgenus *Phyllanthodendron* (Hemsl.) Webster *in* Webster & Carpenter (2008: 608).—Type: *Phyllanthus mirabilis* Müll.Arg. (= formerly *Phyllanthodendron mirabile* (Müll.Arg.) Hemsl.) = *Glochidion mirabilis* (Müll.Arg.) R.W.Bouman.

Coccoglochidion Schumann (1905: 292).—Type: *Coccoglochidion erythrococcus* K.Schum. = *Glochidion philippicum* (Cav.) C.B.Rob.

Tetraglochidion Schumann (1905: 291).—Type: *Tetraglochidion gimi* K.Schum = *Glochidion gimi* (K.Schum.) Pax & K.Hoffm.

Diagnostic features: Shrubs (sometimes climbing) or trees, base sometimes succulent, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, sometimes differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base (not) auriculate. *Cataphylls* triangular. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, rarely paniculate. *Staminate flowers*: sepals 4–6; disc absent or sometimes segmented, 5 or 6, then usually alternating with sepals, ligulate; stamens 3–8, filaments connate, anthers elongate, erect, dehiscing vertically, connectives apiculate or not, when apiculate extensions tightly together (pyramidal), separating when flowers get older; pollen subprolate to prolate, 3–6-colporate, colpi monoporate, exine tectate to reticulate; pistillode absent (except in *G. moi* (P.T.Li) R.W.Bouman). *Pistillate flowers*: sepals 2–8, obovate to elliptic; disc absent or segmented, same number as sepals, alternating with sepals; ovary 3–15-locular; styles present or absent, usually connate in a slender or globular column; stigmas usually reduced, seldom free, subentire, bifid or usually completely fused in a cap-like structure. *Fruits* (inflated) capsules, sometimes with soft tissue. *Seeds* trigonous, woody or fleshy, smooth or striate, with or without sarcotesta.

Distribution: Mainland Asia, Malesia, Australia, Pacific.

Note—Former *Phyllanthus* subgenus *Phyllanthodendron* is paraphyletic with the genus *Glochidion* nested within and is therefore synonymized with *Glochidion*. While the former subgenus *Phyllanthodendron* is morphologically distinguishable from *Glochidion*, by retaining it as a separate genus, *Phyllanthus* section *Pseudoactephila* Croizat would also need to be separated. When split this would result in two genera that are only distinguished based on inflorescence structure. Section *Pseudoactephila* is here transferred and raised to subgenus level to resolve the paraphyly of subgenus *Phyllanthodendron* and the previously defined sections are subsumed in the two subgenera. Not all sections have been included in a phylogenetic study so placement in either subgenus *Phyllanthodendron* or *Pseudoactephila* is here based on the presence or absence of specialized floriferous branchlets next to vegetative branchlets.

Glochidion J.R.Forst. & G.Forst. subgenus **Glochidion**

Glochidion J.R.Forst. & G.Forst. subgenus *Glochidion*: Literature and type as under the genus.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, not differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, rarely paniculate. *Staminate flowers*: sepals 5 or 6, spreading to recurving when old; disc absent; stamens 3–8, filaments connate, anthers erect, dehiscing vertically, connectives usually apiculate and apicula tightly together, sometimes broadened into a head; pollen suboblate to prolate, 3–6-colporate, exine reticulate to tectate; pistillode absent. *Pistillate flowers*: sepals 2–8; disc absent; ovary 3–15-locular; stigmas usually connate in a slender or globular column or cap-like structure, apex split into short stigmatic lobes, sometimes free and then stigmas bifid. *Fruits* capsules. *Seeds* trigonous, often with sarcotesta.

Distribution: Mainland Asia, Malesia, Australia, Pacific.

Notes—1. The combination of the genus *Glochidion* with *Phyllanthus* has been made several times in its history. As circumscribed here, subgenus *Glochidion* covers the traditional genus *Glochidion* excluding *Phyllanthodendron*. The relationship with subgenus *Phyllanthodendron* is remarkable as the flowers are very different: whereas the androecium consisting of connate stamens is similar, the absence of a floral disc in subgenus *Glochidion* is a notable distinction. Species of *Glochidion* are well known for their pollination system that involves mutualistic moths (Kato *et al.* 2003), but pollination observations in subgenus *Phyllanthodendron* are limited, with flies possibly implicated as potential pollinators (Kato & Kawakita 2017).

2. Several sections have been proposed for *Glochidion* by Müller (1865b, 1866), but the diagnostic characters, like the number of stamens, or locules in the ovary, overlap between sections. Within the genus (here subgenus) *Glochidion*, the following sections have been proposed: *Hemiglochidion* Müll.Arg., *Glochidiopsis* (Blume) Pax & K.Hoffm., *Scleroglochidion* (Müll.Arg.) Pax & K.Hoffm. and *Tetraglochidion* (K.Schum) Pax & K.Hoffm, but none are retained here. The species in subgenus *Glochidion* are usually difficult to distinguish and keys, where available, mostly rely on minute characters (van Welzen 2007).

3. Aside from morphological similarity between species that are usually quite variable, the phylogeny of *Glochidion* is poorly resolved (Luo *et al.* 2017). Reported branch lengths are often short or result in polytomies, suggesting that the diversification of *Glochidion* might have been a recent event and possibly enhanced by co-evolution with their mutualistic pollinators.

Included species and taxonomic changes: about 340 species, which are not all listed here. Transfers of *Glochidion* species to the genus *Phyllanthus* by Wagner & Lorence (2011) and Govaerts (2018) are reversed and treated below. The Indian species of subgenus *Glochidion* that were transferred to *Phyllanthus* by Chakrabarty & Balakrishnan (2009), were reinstated following Chakrabarty & Balakrishnan (2018).

Glochidion acuminatissimum Airy Shaw (1972: 55), homotypic synonym: *Phyllanthus lalongatanus* Govaerts (2018: 95).

Glochidion acustylum Airy Shaw (1980b: 591), homotypic synonym: *Phyllanthus acustylus* (Airy Shaw) Govaerts (2018: 94).

Glochidion alstonii Airy Shaw (1981: 600), homotypic synonym: *Phyllanthus alstonii* (Airy Shaw) Govaerts (2018: 94).

Glochidion alticola Airy Shaw (1972: 8), homotypic synonym: *Phyllanthus alticola* (Airy Shaw) Govaerts (2018: 94).

Glochidion aluminescens Airy Shaw (1972: 16), homotypic synonym: *Phyllanthus aluminescens* (Airy Shaw) Govaerts (2018: 94).

Glochidion ambiguum Airy Shaw (1972: 62), homotypic synonym: *Phyllanthus ambiguus* (Airy Shaw) Govaerts (2018: 94).

Glochidion amentuligerum (Müller 1865a: 390) Croizat (1942b: 46). Basionym: *Phyllanthus amentuliger* Müll. Arg.

Glochidion andersonii Airy Shaw (1974: 287), homotypic synonym *Phyllanthus sarawakensis* Govaerts (2018: 95).

Glochidion anfractuosum Gibbs (1909: 168), homotypic synonym: *Phyllanthus anfractuosus* (Gibbs) Wagner & Lorence (2011: 69).

Glochidion angulatum Robinson (1909: 91), homotypic synonym: *Phyllanthus malesianus* Govaerts (2018: 95).

Glochidion apodogynum Airy Shaw (1972: 44), homotypic synonym: *Phyllanthus apodogynus* (Airy Shaw) Govaerts (2018: 94).

Glochidion atalotrichum Smith (1967: 74; homotypic synonym: *Phyllanthus atalotrichus* (A.C.Sm.) Wagner & Lorence (2011: 70).

Glochidion atrovirens Smith (1981: 481, 491), homotypic synonym: *Phyllanthus atrovirens* (A.C.Sm.) Wagner & Lorence (2011: 70).

Glochidion bracteatum Gillespie (1932: 15), homotypic synonym: *Phyllanthus bracteatus* (Gillespie) Wagner & Lorence (2011: 70).

Glochidion brothersonii Florence (1997a: 68), homotypic synonym: *Phyllanthus brothersonii* (J.Florence) Wagner & Lorence (2011: 70).

Glochidion brunnescens Smith (1981: 491), homotypic synonym: *Phyllanthus brunnescens* (A.C.Sm.) Wagner & Lorence (2011: 71).

Glochidion calciphilum Croizat (1942b: 46), homotypic synonym: *Phyllanthus calciphilus* (Croizat) Wagner & Lorence (2011: 71).

Glochidion christophersenii Croizat (1943a: 213), homotypic synonym: *Phyllanthus christophersenii* (Croizat) Wagner & Lorence (2011: 71).

Glochidion cleistanthoides Fosberg *in* Fosberg & Oliver (1991: 263), homotypic synonym: *Phyllanthus cleistanthoides* (Fosberg) Wagner & Lorence (2011: 71).

Glochidion comitum Florence (1997b: 29), homotypic synonym: *Phyllanthus comitus* (J.Florence) Wagner & Lorence (2011: 72).

Glochidion collinum Smith (1981: 494), homotypic synonym: *Phyllanthus vitilevuensis* Wagner & Lorence (2011: 90).

Glochidion concolor Müller (1863: 62), homotypic synonym: *Phyllanthus concolor* (Müll.Arg.) Müller (1865a: 374).

Glochidion cordatum Seemann ex Müller (1863: 64), homotypic synonym: *Phyllanthus cordatus* (Seem. ex Müll.Arg.) Müller (1865a: 376).

Glochidion cuspidatum (Müll.Arg.) Pax (1898: 645), homotypic synonym: *Phyllanthus cuspidatus* Müller (1865a: 377).

Glochidion emarginatum Moore (1933: 30), homotypic synonym: *Phyllanthus emarginatus* (J.W.Moore) Wagner & Lorence (2011: 73).

Glochidion euryoides Smith (1952: 373), homotypic synonym: *Phyllanthus euryoides* (A.C.Sm.) Wagner & Lorence (2011: 74).

Glochidion gillespiei Croizat (1942b: 46), homotypic synonym: *Phyllanthus gillespiei* (Croizat) Wagner & Lorence (2011: 74).

Glochidion gimi (Schumann 1905: 291); Pax & Hoffmann (1931: 58) Basionym: *Tetraglochidion gimi* K.Schum., homotypic synonym: *Phyllanthus gimi* (K.Schum.) Govaerts (2018: 94).

Glochidion grantii Florence (1996: 250), homotypic synonym: *Phyllanthus grantii* (J.Florence) Wagner & Lorence (2011: 74).

Glochidion grayanum (Müller 1865a: 380) Florence (1996: 253), homotypic synonym: *Phyllanthus grayanus* Müll.Arg.

Glochidion heterodoxum (Müller 1866: 321) Pax & Hoffmann (1931: 58), homotypic synonym: *Phyllanthus heterodoxus* Müll.Arg.

Glochidion hivaoaense Florence (1997a: 74), homotypic synonym: *Phyllanthus hivaoaensis* (J.Florence) Wagner & Lorence (2011: 74).

Glochidion hosokawae Fosberg *in* Fosberg & Oliver (1991: 261), homotypic synonym: *Phyllanthus hosokawae* (Fosberg) Wagner & Lorence (2011: 75).

Glochidion huahineense Florence (1997a: 75), homotypic synonym: *Phyllanthus huahineensis* (J.Florence) Wagner & Lorence (2011: 77).

Glochidion inusitatum Smith (1981: 493), homotypic synonym: *Phyllanthus inusitatus* (A.C.Sm.) Wagner & Lorence (2011: 77).

Glochidion kanehirae Hosokawa (1935: 22), homotypic synonym: *Phyllanthus* k*anehirae* (Hosok.) Wagner & Lorence (2011: 77).

Glochidion longfieldiae (Riley 1926: 55) Brown (1935: 141), homotypic synonym: *Phyllanthus longfieldiae* L.Riley.

Glochidion macrosepalum Hosokawa (1935: 21), homotypic synonym: *Phyllanthus macrosepalus* (Hosok.) Wagner & Lorence (2011: 78).

Glochidion manono Baillon ex Müller (1863: 65), homotypic synonym: *Phyllanthus manono* (Baill. ex Müll.Arg.) Müller (1865a: 377).

Glochidion marchionicum Brown (1935: 142), homotypic synonym: *Phyllanthus marchionicus* (F.Br.) Wagner & Lorence (2011: 79).

Glochidion marianum Müller (1863: 65), homotypic synonym: *Phyllanthus mariannensis* Wagner & Lorence (2011: 79), non *Phyllanthus*

marianus Müller (1863: 17).

Glochidion melvilleorum Airy Shaw (1971: 487), homotypic synonym: *Phyllanthus melvilleorum* (Airy Shaw) Wagner & Lorence (2011: 81).

Glochidion multilobum Smith (1981: 493), homotypic synonym: *Phyllanthus multilobu*s (A.C.Sm.) Wagner & Lorence (2011: 81).

Glochidion nadeaudii Florence (1996: 253), homotypic synonym: *Phyllanthus nadeaudii* (J.Florence) Wagner & Lorence (2011: 81).

Glochidion orohenense Moore (1940: 6), homotypic synonym: *Phyllanthus orohenensis* (J.W.Moore) Wagner & Lorence (2011: 81).

Glochidion palauense Hosokawa (1935: 22), homotypic synonym: *Phyllanthus otobedii* Wagner & Lorence (2011: 81), non *Phyllanthus palauensis* Hosokawa (1935: 19).

Glochidion papenooense Florence (1996: 254), homotypic synonym: *Phyllanthus papenooensis* (J.Florence) Wagner & Lorence (2011: 83).

Glochidion pitcairnense (Brown 1935: 142) H.St.John in St. John & Philipson (1962: 187), Basionym: *Glochidion taitense* Baill. ex Müll. Arg. var. *pitcairnensis* F.Br., homotypic synonym: *Phyllanthus pitcairnensis* (F.Br.) Wagner & Lorence (2011: 83).

Glochidion podocarpum (Müller 1865a: 388) Robinson (1911: 330), homotypic synonym: *Phyllanthus podocarpus* Müll.Arg.

Glochidion ponapense Hosokawa (1935: 24), homotypic synonym: *Phyllanthus ponapensis* (Hosok.) Wagner & Lorence (2011: 84).

Glochidion moorei Li (1982: 117), homotypic synonym: *Phyllanthus raiateaensis* Wagner & Lorence (2011: 84).

Glochidion raivavense Brown (1935: 142), homotypic synonym: *Phyllanthus raivavensis* (F.Br.) Wagner & Lorence (2011: 85).

Glochidion rapaense Florence (1996: 258), homotypic synonym: *Phyllanthus rapaensis* (J.Florence) Wagner & Lorence (2011: 85).

Glochidion myrtifolium Moore (1963: 10), homotypic synonym: *Phyllanthus st-johnii* Wagner & Lorence (2011: 86).

Glochidion samoanus (Müller (1866: 289) R.W.Bouman, *comb. nov.*, *stat. nov.* Basionym: *Phyllanthus ramiflorus* (J.R.Forst. & G.Forst.) Müll.Arg. var. *samoanus* Müll.Arg., homotypic synonym: *Phyllanthus samoanus* (Müll.Arg.) Wagner & Lorence (2011: 86).

Glochidion seemannii Müller (1863: 63), homotypic synonym: *Phyllanthus seemannii* (Müll.Arg.) Müller (1865a: 374).

Glochidion senyavinianum Glassman (1952: 71), homotypic synonym: *Phyllanthus senyavinianus* (Glassman) Wagner & Lorence (2011: 87).

Glochidion sessilis (Warburg 1891: 357) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sessilis* Warb.

Glochidion taitense Baillon ex Müller (1863: 66), homotypic synonym: *Phyllanthus taitensis* (Baill. ex Müll.Arg.) Müller (1865a: 380).

Glochidion temehaniense Moore (1963: 15), homotypic synonym: *Phyllanthus temehaniensis* (J.W.Moore) Wagner & Lorence (2011: 88).

Glochidion tuamotuense Florence (1997a: 98), homotypic synonym: *Phyllanthus tuamotuensis* (J.Florence) Wagner & Lorence (2011: 89).

Glochidion vitiense (Müller 1865a: 374) Gillespie (1932: 17), homotypic synonym: *Phyllanthus vitiensis* Müll.Arg.

Glochidion websteri Fosberg *in* Fosberg & Oliver (1991: 262), homotypic synonym: *Phyllanthus websteri* (Fosberg) Wagner & Lorence (2011: 90).

Glochidion wilderi Florence (1997a: 99), homotypic synonym: *Phyllanthus wilderi* (J.Florence) Wagner & Lorence (2011: 90).

Glochidion J.R.Forst. & G.Forst. subgenus **Phyllanthodendron** (Hemsl.) R.W.Bouman, *comb. nov*.

Phyllanthodendron Hemsley (1898: t. 2563); Ridley (1924: 205); Croizat (1942a: 33); Li (1987b: 8).—*Phyllanthus* L. section *Phyllanthodendron* (Hemsl.) Beille (1925: 160); Pax & Hoffmann (1931: 63).—*Phyllanthus* L. subgenus *Phyllanthodendron* (Hemsl.) Webster (2008: 608).—Type: *Phyllanthodendron mirabile* (Müll.Arg.) Hemsl. (formerly *Phyllanthus mirabilis* Müll.Arg.) = *Glochidion mirabilis* (Müll.Arg.) R.W.Bouman.

Phyllanthodendron Hemsl. section *Euphyllanthodendron* Croizat (1942a: 33), *nom. inval*.—Type: *Phyllanthus mirabilis* Müll.Arg.(see Airy Shaw (1960: 469) and note 2) = *Glochidion lingulatum* (Beille) R.W.Bouman.

Phyllanthodendron Hemsl. section *Calophyllum* Croizat (1942a: 33).—Type: *Phyllanthus anthopotanicum* Hand.-Mazz (formerly *Phyllanthodendron anthopotamicum* (Hand.-Mazz.) Croizat) = *Glochidion anthopotanicum* (Hand.-Mazz) R.W.Bouman.

Diagnostic features: Shrubs (sometimes climbing) or trees, base sometimes succulent, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6, free, ligulate; stamens 3 (or 4), filaments connate, anthers erect, dehiscing vertically, connectives usually apiculate; pollen subprolate, 4-colporate, colpi monoporate, exine reticulate; pistillode absent. *Pistillate flowers*: sepals 5 or 6, oblong, obovate-elliptic; disc glands 5 or 6, free, ligulate; ovary 3-locular; styles present or absent; stigmas bifid or subentire. *Fruits* (inflated) capsules. *Seeds* trigonous, striate, hollow ventrally.

Distribution: Mainland Asia.

Notes—1. *Phyllanthodendron* Hemsl. was a separate genus that was retained in the Flora of China (Li 1987b), while other treatments include it as a section within *Phyllanthus* (see treatment of species in Beille 1925; Chantaranothai 2007). Several sections have been defined, often based on the habit or number of sepals and stamens, but the differences are often small. These sections are here subsumed, with *Phyllanthus* sections *Phyllanthodendron* and *Calophyllum* placed in subgenus *Phyllanthodendron* on account of the specialized floriferous branchlets. Sections *Tetrandrum*, *Pseudoactephila* and *Arachnodes* do not have floriferous branchlets and are subsumed in subgenus *Pseudoactephila*.

2. Croizat (1942a) divided the genus *Phyllanthodendron* Hemsl. in three sections, section *Phyllanthodendron*, *Pseudoactephila* and *Calophyllum* Croizat. *Phyllanthus lingulatus* Beille was incorrectly designated as the type of section *Phyllanthodendron* (type of the genus Phyllanthodendron is *P. mirabilis* (Müll.Arg.) Hemsl.), which was later corrected by Airy Shaw (1960).

Included species and taxonomic changes (5 spp.):

Glochidion anthopotamicus (Handel-Mazzetti 1931: 223) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus anthopotamicus* Hand.-Mazz.

Glochidion dongmoensis (Thin 1992: 16) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dongmoensis* Thin.

Glochidion dunnianus (Léveillé 1911: 324) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron dunnianum* H.Lév., homotypic synonym: *Phyllanthus dunnianus* (H.Lév.) Hand.-Mazz. ex Rehder (1933: 230).

Glochidion kaweesakii (Pornpongrungrueng, Chantaranothai & Parnell *in* Pornpongrungrueng *et al.* 2017: 572) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kaweesakii* Pornp., Chantar. & J.Parn.

Glochidion mirabilis (Müller 1864: 513) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mirabilis* Müll.Arg.

Glochidion J.R.Forst. & G.Forst. subgenus **Pseudoactephila** (Croizat) R.W.Bouman, *stat. et comb. nov.*

Phyllanthus L. subgenus *Phyllanthodendron* (Hemsl.) G.L.Webster section *Pseudoactephila* Croizat (1942a: 33).—Type: *Phyllanthus roseus* (Craib & Hutch.) Beille (= *Phyllanthodendron roseum* Craib & Hutch. = *Glochidion roseum* (Craib & Hutch.) R.W.Bouman).

Uranthera Pax & Hoffmann (1911: 95), *nom. illeg*., non *Uranthera* Naudin (1845: 189).—Type: *Uranthera siamensis* Pax & K.Hoffm. (= formerly Phyllanthus roseus (Craib & Hutch.) Beille) = *Glochidion roseum* (Craib & Hutch.) R.W.Bouman.

Arachnodes Gagnepain (1950: 32).—*Phyllanthus* L. subgenus *Phyllanthodendron* (Hemsl.) G.L.Webster section *Arachnodes* (Gagnep.) Airy Shaw (1960: 470).—Type: *Arachnodes chevalieri* Gagnep. (non *Glochidion chevalieri* Beille 1927: 615) (= formerly *Phyllanthus arachnodes* Govaerts & Radcl.-Sm.) = *Glochidion arachnodes* (Govaerts & Radcl.-Sm.) R.W.Bouman.

Phyllanthodendron Hemsl. section *Tetrandrum* Li (1987b: 8).—Type: *Phyllanthodendron moi* (P.T.Li) P.T.Li (= formerly *Phyllanthus moi* P.T.Li) = *Glochidion moi* (P.T.Li) R.W.Bouman.

Diagnostic features: Shrubs, sometimes twining, monoecious, branching phyllanthoid, branchlets pinnatiform, not differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, bisexual, flowers crowded in long-pedicelled clustered fascicles. *Staminate flowers*: sepals 4–6; disc glands 4–6, free, ligulate; stamens 3 or 4, filaments connate, anthers erect, dehiscing vertically, connectives usually apiculate; pollen subprolate, 4-colporate, colpi monoporate, exine reticulate; pistillode absent (except in *G. moi*). *Pistillate flowers*: sepals 5 or 6; disc glands 5 or 6, free, ligulate; ovary 3-locular; styles?; stigmas bifid to entire. *Fruits* (inflated) capsules. *Seeds* trigonous.

Distribution: Mainland Asia.

Note—Phyllanthodendron section *Tetrandrum* was a monotypic section for a species with a 4-merous staminate flower that is here subsumed as the number of sepals is considered variable within the subgenus. *Phyllanthodendron* section *Arachnodes* was mainly distinguished by its twining habit.

Included species and taxonomic changes (14 spp.):

Glochidion arachnodes (Govaerts & Radcliffe-Smith 1996: 175) R.W.Bouman, *comb. nov.* Basionym: *Arachnodes chevalieri* Gagnepain (1950: 32, non *Glochidion chevalieri* Beille 1927: 615), homotypic synonym: *Phyllanthus arachnodes* Govaerts & Radcl.-Sm.

Glochidion breyniopsis Esser & R.W.Bouman, *nom. nov.* (non *G. breynioides* Robinson 1909: 95), Basionym: *Phyllanthodendron breynioides* P.T.Li (1987b: 6), homotypic synonym: *Phyllanthus breynioides* (P.T.Li) Govaerts & Radcliffe-Smith (1996: 176).

Glochidion carinatum (Beille 1925: 160) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carinatus* Beille, homotypic synonym: *Phyllanthodendron carinatum* (Beille) Croizat (1942a: 36).

Glochidion caudatifolium (Li 1987b: 7) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron caudatifolium* P.T.Li, homotypic synonym: *Phyllanthus lii* Govaerts & Radcliffe-Smith (1996: 177).

Glochidion lativenium (Croizat 1942a: 36) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron lativenium* Croizat, homotypic synonym: *Phyllanthus lativenius* (Croizat) Govaerts & Radcliffe-Smith (1996: 177).

Glochidion lingulatum (Beille 1925: 161) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lingulatus* Beille.

Glochidion moi (Li 1983: 167) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus moi* P.T.Li.

Glochidion orbicularifolium (Li 1987b: 5) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron orbicularifolium* P.T.Li, homotypic synonym: *Phyllanthus orbicularifolius* (P.T.Li) Govaerts & Radcliffe-Smith (1996: 177).

Glochidion petraeum (Li 1987b: 4) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron petraeum* P.T.Li, homotypic synonym: *Phyllanthus guanxiensis* Govaerts & Radcliffe-Smith (1996: 176).

Glochidion poilanei (Beille 1925: 162) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poilanei* Beille.

Glochidion minutiflorum (Ridley 1911: 169) R.W.Bouman, *comb. nov.* Basionym: *Cleistanthus minutiflorus* Ridl., homotypic synonym: *Phyllanthus ridleyanus* Airy Shaw (1972: 323).

Glochidion roseum (Craib & Hutchinson 1910: 23) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron roseum* Craib & Hutch., homotypic synonym: *Phyllanthus roseus* (Craib & Hutch.) Beille (1927: 590).

Glochidion rubicundum (Beille 1925: 162) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rubicundus* Beille.

Glochidion yunnanense (Croizat 1942a: 36) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron yunnanense* Croizat, homotypic synonym *Phyllanthus yunnanensis* (Croizat) Govaerts & Radcliffe-Smith (1996: 178).

Clade I—Fig. 1, 2N & O (supplementary fig. 1)

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

Breynia Forster & Forster (1776: 145), nom. cons.—Type: *Breynia disticha* J.R.Forst. & G.Forst. (for a more expanded nomenclature of *Breynia* and its subgeneric groups, see van Welzen *et al.* 2014).

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous. *Inflorescences* axillary, usually unisexual fascicles, sometimes larger compound inflorescences. *Staminate flowers* discoid or campanulate to turbinate; sepals 6, usually connate for half to whole length with some exceptions, with sepal scales (absent in *B. granulosa* (Airy Shaw) Welzen & Pruesapan, *B. kerrii* (Airy Shaw) Welzen & Pruesapan, *B. pierrei* (Beille) Welzen & Pruesapan, *B. pulchella* (Airy Shaw) Welzen & Pruesapan, *B. shawii* (Welzen) Welzen & Pruesapan, *B. subterblanca* (C.E.C.Fisch.) C.E.C.Fisch., and *B. rostrata* Merr.); disc absent; stamens 3, filaments connate, free parts horizontal or oblique or fused and vertical; anthers dehiscing lengthwise (same as vertically in other genera); pollen 4–16-colporate, colpi diploporate, exine (micro) reticulate, tectate; pistillode absent. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular, sometimes with an apical rim; styles absent; stigmas bifid or entire, horizontal to erect, sometimes reduced. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.

Distribution: Mainland Asia (to China), Malesia, Australia, Pacific.

Note—Mainly distinguished from the genus *Synostemon* by the subglobose ovaries that are usually flattened apically, bifid stigmas that are usually split for more than half of their length and smooth seeds (van Welzen *et al.* 2014). Species in the genus *Synostemon* have ovate ovaries with an obtuse or lobed apex, usually entire or only slightly bifid stigmas (less than half of their length) and seeds ornamented (van Welzen *et al.* 2014).

Breynia J.R.Forst. & G.Forst. subgenus **Breynia**

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

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Inflorescences* axillary, usually unisexual fascicles. *Staminate flowers* discoid or campanulate to turbinate; sepals 6, connate for half to almost completely; disc absent; stamens 3, filaments connate, connective also sometimes fused; anthers dehiscing vertically; pollen 4–12-colporate, colpi diploporate, exine (micro-) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular, sometimes with an apical rim; styles absent; stigmas bifid or entire, horizontal to erect, sometimes reduced in size. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.

Distribution: Mainland Asia, Malesia, Australia, Pacific.

Breynia J.R.Forst. & G.Forst. section **Breynia**

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

Breynia section *Breyniastrum* Baillon (1866: 344).—Lectotype (designated by Esser *in* van Welzen *et al.* 2014): *Breynia stipitata* Müll. Arg.

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Staminate flowers*: campanulate to turbinate; sepals 6, usually connate for whole length; disc absent; stamens 3, filaments connate, connective also sometimes fused; anthers dehiscing vertically; pollen 4–12-colporate, colpi diploporate, exine (micro) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular; styles absent; stigmas bifid or entire, horizontal to erect, often reduced in size. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.

Distribution: Mainland Asia, Malesia, Australia, Pacific.

Breynia J.R.Forst. & G.Forst. section **Cryptogynium** (Müll.Arg.) Welzen & Pruesapan

Breynia J.R.Forst. & G.Forst. section *Cryptogynium* (Müll.Arg.) Welzen & Pruesapan *in* van Welzen *et al.* (2014: 89); van Welzen (2017: 90).—Type: *Ceratogynum rhamnoides* Wight = *Breynia quadrangularis* (J.G.Klein ex Willd.) Chakrab. & N.P.Balakr.

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Staminate flowers* discoid; sepals 6, usually connate for half to whole length with some exceptions; disc absent; stamens 3, filaments connate, connective also sometimes fused, anthers dehiscing horizontally to vertically; pollen 6–12-colporate, colpi diploporate, exine (micro) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular, sometimes with an apical rim; styles absent; stigmas bifid, horizontal to erect. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.

Distribution: Mainland Asia, Malesia.

Breynia J.R.Forst. & G.Forst. subgenus **Sauropus** (Blume) Welzen & Pruesapan

Breynia J.R.Forst. & G.Forst. subgenus *Sauropus* (Blume) Welzen & Pruesapan in van Welzen *et al.* (2014: 91).—Type: *Sauropus stipitatus* Hook.f. = *Breynia gynophora* Welzen & Pruesapan.

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Inflorescences* axillary, usually unisexual fascicles, sometimes larger and longer compound inflorescences. *Staminate flowers* discoid; sepals 6, usually connate for half to completely with some exceptions; disc absent; stamens 3, filaments connate, connectives horizontal, with thecae hanging underneath, dehiscing vertically; pollen 8–16-colporate, colpi diploporate, exine (micro) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular; styles absent; stigmas bifid, horizontal to ascending. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.

Distribution: Mainland Asia, Malesia, Australia.

Note—Other characters that might be useful for distinguishing this group from other *Breynia* species include the considerably large leaf size in most species, with the exception of *B. carnosa* Welzen & Pruesapan (van Welzen *et al.* 2014).

Synostemon F.Muell.

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

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid or subphyllanthoid, branchlets pinnatiform. *Brachyblasts* absent (except in *S. rigens* F.Muell.). *Cataphyllary stipules* triangular, indurate or membranous, base not auriculate. *Cataphylls* triangular to elongate. *Inflorescences* axillary, usually unisexual fascicles. *Staminate flowers*: campanulate to turbinate; sepals 6, connate or free, without sepal scales (except present in *S. bacciformis* (L.) G.L.Webster and *S. anemoniflorus* (J.T.Hunter & J.J.Bruhl) I.Telford & Pruesapan); disc absent; stamens 3, filaments connate, connectives often fused, apiculate with apicula free or fused in a cap; anthers dehiscing vertically; pollen 3–8-colporate, colpi diploporate, exine (micro) reticulate, heterobrochate; pistillode absent. *Pistillate flowers*: sepals

6; disc absent; ovary 3-locular, sometimes with a (slight) rim; styles absent; stigmas bifid (except in *S. elachophyllus* (F.Muell.) Airy Shaw), erect or spreading. *Fruits* capsules, schizocarpic, subglobose or ovoid, longer than wide. *Seeds* trigonous, prominently sculptured.

Distribution: Mainly Australia with one species also occurring in Malesia (*Synostemon sphenophyllus* Airy Shaw in Papua New Guinea) and one widespread tropical coastal Indian and western Pacific Ocean species, *S. bacciformis*.

Notes—Synostemon has recently been enlarged through close taxonomic study (Telford & Naaykens 2015; Telford *et al.* 2015, 2016, 2019) and consists of about 41 species (one unpublished). Only species that were still not transferred are listed below.

Included species and taxonomic changes: Five previously untreated species of *Sauropus* are transferred here to *Synostemon* to complete the reinstatement of *Synostemon*.

Synostemon anemoniflorus (Hunter & Bruhl 1997a: 662) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus anemoniflorus* J.T.Hunter & J.J.Bruhl.

Synostemon arenosus (Hunter & Bruhl 1997b: 166) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus arenosus* J.T.Hunter & J.J.Bruhl.

Synostemon brunonis (Moore 1920: 213) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus brunonis* (S.Moore) Airy Shaw (1980c: 672).

Synostemon huntii (Ewart & Davies 1917: 164) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus huntii* (Ewart & O.B.Davies) Airy Shaw (1980c: 679).

Synostemon paucifolius (Hunter & Bruhl 1997b: 172) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus paucifolius* J.T.Hunter & J.J.Bruhl.

Doubtful species

Phyllanthus petiolaris Roxb. was described by Roxburgh (1832), but he only mentioned the habit and the presence of flowers. More details on the flowers are necessary to place it in any genus. Based on its location, the species could be in any of these genera: *Cathetus*, *Nymphanthus* or *Emblica*. Balakrishnan & Chakrabarty (2007) treat this as an unplaced name.

Discussion & conclusions

This treatment is a proposed solution to the paraphyly of the genus *Phyllanthus*. By reinstating nine other genera separated from *Phyllanthus* along with other subgeneric realignments we feel confident that this classification is a much better reflection of the evolutionary history of this group. All genera proposed here are monophyletic in our phylogenetic analyses (Suppl Fig.1; Bouman *et al.* 2021) and might be used for further extensive studies. Many genera have not received a full taxonomic treatment as a group, and future revisions could result in the recognition of new species. Some of relationships found in Bouman *et al.* (2021) were surprising and in contrast with morphology based classification as the morphological character states used are of parallel origin. These are interesting for further study (such as the relation between groups within the genus *Glochidion*).

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Appendix 1. Species specific differences with previous classification by Bouman *et al.* (2018: table 2).

Several species were treated in the main text in other subgeneric groups differing from the species table presented by Bouman *et al.* (2018b). In this appendix we briefly explain minor changes and species transfers that are not treated in the main text, but were the result of new information.

Australian species of *Dendrophyllanthus*

Three Australian species here treated in the genus *Cicca* (*C. lacunella*, *C. lacunaria* and *C. erwinii*) were originally placed in *Phyllanthus* section *Antipodanthus* or *Lysiandra*, but were found to be nested in the clade of *Dendrophyllanthus* (supplementary fig. 1).

Species by Blanco (1837, 1845)

Two species described by Blanco (1845) were brought to our attention by P. Pelser (pers. comm.) while discussing identifications for Co's Digital Flora of the Philippines (Pelser *et al.*, 2011 onwards). At the time we had seen no material of these species and they were treated by Müller (1866) in a section that seemed to be synonymized under the genus *Flueggea* Barker & Welzen 2010). However, this was a consequence of a wrong identification of the type material of *P. glaucus*, which was corrected in Chakrabarty & Balakrishnan (2018). The two following species were originally published in the genus *Kirganelia* and seemed valid, but were reduced to synonymy by Merrill (1918), which is followed here until more material is collected. This means that we still treat both names as synonyms and do not include them in the genus *Kirganelia*. Merrill (1918) synonymized *P. nigrescens* (Blanco) Müll.Arg. under *Glochidion lancifolium* and *P. pumilus* (Blanco) Müll.Arg. as *P. niruri* (though *P. amarus* or *P. debilis*, here *M. amara* and *M. debilis* are more likely).

Species by Koorders

The affinities of *P. celebicus* Koord. and *P. minahassae* Koord. were not known during the study of Bouman *et al.* (2018b). Subsequent study of the type material showed these species to have the characteristic flowers of species in *Phyllanthus* subgenus *Eriococcus* (Bouman *et al.* 2019), which are all transferred here to the reinstated genus *Nymphanthus*.

Indian species of *Phyllanthus* s.l.

The subgeneric placements in Chakrabarty & Balakrishnan (2018) mostly follow Webster (1956, 1957, 1958), but later modifications proposed by Brunel (1987) or Ralimanana & Hoffmann (2011, 2013) are not incorporated. Phyllanthoid branching, which is a phylogenetically informative character, is mentioned in the descriptions of several groups, but not applied consistently. Without the inclusion of pictures of the flowers and specimens with clear depiction of the branching system, many placements here await inclusion of a palynological or phylogenetic study.

Phyllanthus ajmerianus L.B.Chaudhary & R.R.Rao (here *Moeroris ajmerianus* (L.B.Chaudhary & R.R.Rao) R.W.Bouman) is treated here in *Moeroris* subgenus *Tenellanthus* on account of its 5-merous staminate flower with 5 stamens that are partially connate at the base (see Chaduhary & Rao 2006). The longitudinally striate seed is also common in the genus *Moeroris* and subgenus *Tenellanthus* contains more cryptophytic species.

Phyllanthus brevipes Hook.f. was treated in *Phyllanthus* subgenus *Afroswartziani* (Bouman *et al.* 2018b), but is probably a species of *Cathetus* subgenus *Macraea*. Chakrabarty & Balakrishnan (2018) treat this species in *Phyllanthus* subgenus *Phyllanthus*, but mention that laminate leaves are present on all axes (non-phyllanthoid branching?) and it is therefore treated here in the genus *Cathetus*. The staminate flower has 3 partially connate stamens and the pistillate disc is 6 lobed, but not segmented which is more typical for *Cathetus* subgenus *Macraea* than the genus *Nellica*.

Phyllanthus griffithii Müll.Arg. was listed in Bouman *et al.* (2018b), but *P. stylosus* Griff. was published earlier and is a valid epithet. *Phyllanthus griffithii* is therefore listed here as a synonym of *P. stylosus* following treatments that consider this to be the same species (Chakrabarty & Balakrishnan 2018). Specimens attributed to *P. stylosus* bear leaves on all axes (specimen W. Griffith 4822 deposited at K with barcodes K000246565, K000246566), only basally connate stamens and an entire pistillate disc (Chakrabarty & Balakrishnan 2018). It is treated here in *Cathetus* subgenus *Macraea*.

Phyllanthus hakgalensis Thwaites ex Trimen was tentatively placed by Webster (1997) in section *Paraphyllantus* (now genus *Nellica*), but he mentioned that this species has an entire pistillate disc, which is more typical for *Cathetus* subgenus *Macraea*. Based on the entire pistillate disc and three free stamens in the staminate flower, it is here treated in *Cathetus* subgenus *Macraea*. Verwijs *et al.* (2019) did not include this species in their treatment of subgenus

Macraea, but did discuss similarities. Chakrabarty & Balakrishnan (2018) treated this species in *Phyllanthus* subgenus *Eriococcus* (now genus *Nymphanthus*) based on descriptions by Alston (1931), which would need to be confirmed. Unfortunately, this species is only known from the type specimen. Webster (1997) described the phyllotaxis as spiral, which could be plesiomorphic or this species might be related to *Cicca* subgenus *Betsileani* (Jean F.Brunel) Ralim. & Petra Hoffm. (very unlikely considering its geographical range). Perhaps the pollen could be informative, but this species has not been included in any previous palynological study.

Phyllanthus leschenaultii Müll.Arg. has phyllanthoid branching and is described as having partially connate filaments in the staminate flower with horizontally dehiscing orbicular anthers (Chakrabarty & Balakrishnan 2018). This is comparable to *Moeroris* subgenus *Moeroris*. However, we could not confidently confirm the branching type and, less likely, it could also be a species of *Cathetus* subgenus *Macraea*.

Phyllanthus mozambicensis Gand. was still listed as an accepted species in Govaerts *et al.* (2000) and Bouman *et al.* (2018b), but Radcliffe-Smith (1996) treats it as a synonym of *P. parvulus*. As this epithet has to our knowledge not been reinstated as a separate species, it is only treated as a synonym here and not separately transferred to the genus *Moeroris*.

Phyllanthus parvifolius Buch.-Ham. ex D.Don is treated similarly to *P. stylosus* and *P. praetervisus* and placed in *Cathetus* subgenus *Macraea* (see Mitra & Sanjappa 2003 for more information on these complex species). The difficulty in assigning these species also lies in the apparent fusion of the filaments, which can be variable in species of *Cathetus* subgenus *Macraea*. A palynological study by Sagun & Van der Ham (2003) mentions unpublished data from Punt gouping the pollen of *P. griffithii* (here *C. stylosus*), *P. parvifolius* and *P. praetervisus* in one type that approaches pantoporate pollen (as seen in *Cathetus* subgenus *Cathetus*).

Phyllanthus pseudoparvifolius R.L.Mitra & Sanjappa is treated in the genus *Cathetus*. The free stamens in the staminate flower and ornamentation of the seeds are similar to other species of *Cathetus* subgenus *Macraea*, and it is therefore included here. Unfortunately, this placement is also tentative and awaits a palynological or phylogenetic study.

The syntypes of *Phyllanthus praetervisus* Müll.Arg. in BR seem to be a mixture. One appears to have non-phyllanthoid branching with leaves on all axes (BR0000013336042) and the other has phyllanthoid branching with fascicled branchlets (BR0000005100972). *Phyllanthus praetervisus* is tentatively placed in *Cathetus* subgenus *Macraea*, but the material listed in Chakrabarty & Balakrishnan (2018) as isotypes do not appear to be from the same collection.

Phyllanthus pendulus Roxb. is placed in the genus *Moeroris*, but there are only some meagre literature descriptions available (see Chakrabarty & Balakrishnan 2007, 2018).

Individual cases (treated alphabetically)

Phyllanthus caesius Airy Shaw & G.L.Webster was originally placed by Airy Shaw & Webster (1971) in subgenus *Kirganelia*, but later treated in subgenus *Gomphidium* (Airy Shaw 1980). After reviewing the isotype stored at L (L0016415), we decided to follow the latter placement in subgenus *Gomphidium* (here in genus *Dendrophyllanthus*).

Phyllanthus caudatifolius Merr. was placed in subgenus *Kirganelia* with some doubt and after seeing the type specimen *R.C. McGregor 43867* from K (K001056679) and dissecting a flower, it seems better placed in what we consider *Dendrophyllanthus* section *Leptonema*.

Phyllanthus dumetosus Poir. was treated in subgenus *Kirganelia* and listed as occurring in the Philippines, but this was a mistake in the JSTOR's Global Plants database (https://plants.jstor.org/). After studying material of this species from K, we treat it in the genus *Moeroris* subgenus *Tenellanthus*.

Phyllanthus fallax Müll.Arg. is treated in *Phyllanthus* section *Loxopodium* since the type seems to have non-phyllanthoid branching.

Phyllanthus lasiogynus Müll.Arg. is not further placed in any subgenus, but appears to have phyllanthoid branching and is probably better suited to stay in the genus *Phyllanthus*.

Phyllanthus lunifolius Gilbert & Thulin is doubtfully treated in the genus *Moeroris*, mainly because of its distribution. Staminate flowers are needed to confirm placement. It has large brachyblasts, but these also occur in the genus *Cicca*. Its ericoid leaves are unusual within the African species of *Phyllanthus* and its relation to other species is unknown.

Phyllanthus polyphyllus Willd. is treated as synonym of *Emblica racemosus* following Chakrabarty & Balakrishnan (2017 as *Phyllanthus racemosus*).

Phyllanthus pseudocarunculatus Radcl.-Sm. is a later homotypic synonym of Brunel's (1987) *P. carunculatus*.

Both names are based for the same material and Radcliffe-Smith (1996) published his later name under the assumption that Brunel´s name (1987) was not validly published.

Phyllanthus rupicola Elmer is treated in the genus *Emblica* since it bears great similarity to *E. erythrotrichus*. However, the staminate flower was never described and is needed to confirm this placement.

Phyllanthus securinegoides Merr. could also be *Emblica* based on pollen described in Wu *et al.* 2016. The same is true for *P. glochidioides* which has no description of the staminate flower. The Philippine *P. apiculatus* should also be checked to determine whether it belongs in the genus *Dendrophyllanthus* (here done provisionally) or in the genus *Emblica*.

Phyllanthus squamifolius (Lour.) Stokes and *P. villosus* (Lour.) Müll.Arg. were also treated in *Nymphanthus* on account of their geography and because they were originally also treated in that genus. No material was seen of these species and more collections are needed to confirm our placement.

Phyllanthus triphlebius C.B.Rob. is treated in the genus *Nymphanthus*, but its pollen is very different from the other species of this genus (see Wu *et al.* 2016).

Phyllanthus udoricola Radclf.-Sm. was described by Radcliffe-Smith (1996) with *P. pusillus* Jean F.Brunel listed as a invalidly published synonym since Brunel's (1987) thesis was not yet accepted as validly published. However, since his thesis contains a printing company and copies of it have been distributed to several institutes, it can be seen as validly published under article 30.8 of the Shenzhen Code (Turland *et al.* 2018). Brunel (1987). The thesis is now accepted and followed in several studies (Ralimanana & Hoffmann 2011, 2014; Ralimanana *et al.* 2013). Therefore, *P. pusillus* (here transferred to *Moeroris pusillus*) becomes the oldest legitimate name and *P. udoricola* is placed in synonymy.

Phyllanthus vergens Baill. has not yet been placed in any specific subgenus within *Phyllanthus* (Ralimanana & Hoffman, 2011; Ralimanana & Cable, 2020), the staminate flowers with (to five) free stamens suggest an affinity to the genus *Cicca*. The inflorescences borne on leafless branches (Ralimanana & Cable 2020) are also consistent with other species of the genus *Cicca*.

Phyllanthus zippelianus Müll.Arg. is treated in *Kirganelia* since it was described originally with 5 stamens, but more material is needed to confirm our placement.

Appendix 2. GenBank accessions numbers used in phylogenetic analyses. The majority of sequences came from Kathriarachchi *et al.* (2006), Pruesapan *et al.* (2008, 2012), Kawakita & Kato (2009), Falcón *et al.* (2020) and Bouman *et al.* (2021). GenBank accessions from Falcón *et al.* (2020) are highlighted in bold.

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Actephila excelsa	Bouman & Yong RWB057 (HITBC)		MN904188	MN915296	MN916079	
Antidesma bunius	Gent living collection xx0Gent19002015		MN904189		MN916080	
Breynia amoebiflora	Maxwell 90-721 (L)				EU643747	
Breynia amoebiflora	Kerr 19655 (P)	GQ503379	GQ503437	GQ503498		GQ503562
Breynia androgyna (1)	Van Welzen 2006-4 (L)	EU623563	GQ503439	GQ503500	EU643748	GQ503564
Breynia androgyna (3)	Kathriarachchi *et al.* 40 (K)	AY936747	GQ503459	GQ503517		GQ503588
Breynia asteranthos	Esser 99-13 (L)	EU623565		GQ503501	EU643751	
Breynia bicolor	Esser 99-21 (L)	EU623567		GQ503503	EU643754	
Breynia brevipes	Middleton *et al.* 974 (L)	EU623568			EU643755	
Breynia cf. macrantha	Bouman & Yong RWB050 (HITBC)	MN915813	MN904190	MN915297	MN916081	MN915580
Breynia discigera	Takeuchi *et al.* 18873 (L)	EU623550	GQ503410		EU643736	
Breynia discocalyx	Beusekom & Phengklai 566 (L)	GQ503387			EU643757	GQ503569
Breynia disticha (1)	Bouman & Verwijs RWB024 (L)	MN915814	MN904191	MN915298	MN916082	MN915581
Breynia disticha (2)	Yu 63 (L)	MN915815	MN904192	MN915299	MN916083	MN915582
Breynia fruticosa	Bouman *et al.* RWB025 (L)	MN915816	MN904193	MN915300	MN916084	MN915583
Breynia garrettii	Sino-American Guizhou Botanical Expedition 1872 (L)	EU623570	GQ503444	GQ503507	EU643760	GQ503572
Breynia glauca	Pooma *et al.* 2702 (L)	EU623551	GQ503411		EU643737	GQ503532
Breynia hirsuta	Larsen *et al.* 33993 (P)	GQ503391	GQ503445		EU643762	
Breynia kerrii	Van Beusekom & Phengklai 1065 (P)	EU623574	GQ503452		EU643764	GQ503579
Breynia lanceolata	Esser 2001-4 (L)	EU623584			EU643774	
Breynia lithophila	Phonsena *et al.* 5595 (L)		GQ503464	GQ503522		GQ503595
Breynia macrantha	Telford & Bruhl 13107 (L)	GQ503396				
Breynia macrantha	Maxwell 95-1125 (L)				MT551232	
Breynia micrasterias	Erwin & Chai S 27479 (L)	EU623578	GQ503455		EU643768	GQ503582
*Breynia novoguineensis**	Baker *et al.* 37 (L)	EU623549	GQ503409	GQ503472		GQ503530
Breynia oblongifolia	Forster 32745 (NE)	GQ503355	GQ503414	GQ503475		GQ503534
Breynia orbicularis	Soejarto & Southavong 10792 (L)	EU623580	GQ503456	GQ503513	AY936645	GQ503584
Breynia poomae	Phonsena *et al.* 5245 (L)	EU623582	GQ503457	GQ503515	EU643771	GQ503586
Breynia repens	Middleton *et al.* 2287 (L)	GQ503385				GQ503566
Breynia retusa	Kathriarachchi *et al.* 43 (K)				AY936565	
Breynia retusa	Soejarto & Southavong 10783 (L)	GQ503358	GQ503417	GQ503477		GQ503536
Breynia rostrata	Bouman & Yong RWB055 (HITBC)	MN915817	MN904194	MN915301	MN916086	MN915585
Breynia similis (1)	Larsen *et al.* 46639 (L)	GQ503399	GQ503462	GQ503520	EU643778	GQ503592
Breynia similis (2)	Bouman & Yong RWB054 (HITBC)	MN915818	MN904195	MN915302	MN916085	MN915584
Breynia sp. (1)	Middleton 1715 (L)	MN915843	MN904215	MN915327	MN916112	MN915600
Breynia sp. (2)	Tagane *et al.* T570 (L)	MN915844	MN904216	MN915328	MN916113	
Breynia spatulifolia	Wong s.n. (L)	EU623588		GQ503523	AY936647	GQ503596
Breynia stipitata	Chase 14461 (K)				AY552422	
Breynia stipitata	Bruhl 2478 (NE)	GQ503359	GQ503418	GQ503478		GQ503537

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Breynia thorelii	Van Welzen 2006-1 (L)	EU623590	GQ503468	GQ503526	EU643782	GQ503600
Breynia thyrsiflora	Kostermans 765 (L)	EU623591	GQ503469	GQ503527	EU643783	GQ503601
Breynia vestita	Barker & Beaman 70 (L)	EU623553	GQ503419	GQ503480	EU643738	GQ503540
Breynia villosa	Phengklai *et al.* 12122 (BKF)	EU623593			EU643786	
Breynia vitis-idea (1)	Tagane *et al.* V388 (L)	MN915819	MN904184	MN915303	MN916087	
Breynia vitis-idea (2)	Tagane *et al.* V404 (L)	MN915820	MN904185	MN915304	MN916088	MN915586
Breynia vitis-idea (3)	Majaducon 5676 (L)	MN915821	MN904186	MN915305	MN916089	
Breynia vitis-idea (4)	Yu 157 (L)	MN915822	MN904187	MN915306	MN916090	MN915587
Bridelia tomentosa	Bouman & Yong RWB063 (HITBC)		MN904196	MN915307	MN916359	
Cathetus aff. fasciculatus (1)	Bouman & Yong RWB052 (HITBC)	MN915840	MN904250	MN915324	MN916144	MN915601
Cathetus aff. fasciculatus (2)	Bouman & Yong RWB065 (HITBC)	MN915841	MN904251	MN915325	MN916145	MN915602
Cathetus aff. fasciculatus (3)	Bouman & Yong RWB060 (HITBC)	MN915842	MN904252	MN915326	MN916146	MN915603
Cathetus beckleri	Hosking 2680 (NE)	MN915861	MN904231	MN915347	MN916127	MN915618
Cathetus chrysanthus	Munzinger & McPherson 796 (MO)	AY936680			AY936585	
Cathetus fasciculatus	Bouman *et al.* RWB026 (L)	MN915895	MN904262	MN915384	MN916154	MN915648
Cathetus distichus	Harold st. John 17.985 (L)	MN915912	MN904276	MN915404	MN916163	MN915665
Cathetus exilis	Hunter *et al.* 1528 (L)	MN915922	MN904283		MN916362	MN915672
Cathetus filicaulis	Telford 13516 (NE)	MN915923	MN904284	MN915415	MN916170	MN915673
Cathetus gardnerianus	Kathriarachchi *et al.* 42 (K)	AY936694	MN904314	MN915429	AY936598	MN915684
Cathetus glaucophyllus (1)	Van der Brugt 1156 (WAG)	MN915938	MN904317	MN915432	MN916183	MN915687
Cathetus glaucophyllus (2)	Haba 123 (WAG)	MN915939	MN904318	MN915433	MN916340	MN915688
Cathetus kerstingii (1)	Darbyshire 562 (WAG)	MN915950	MN905074	MN915447	MN916189	MN915701
Cathetus kerstingii (2)	Malaisse 14792 (WAG)	MN915951		MN915448		MN915702
Cathetus myrtifolius (1)	Bouman & Liu RWB034 (L)	MN915995	MN904370	MN915495	MN916214	MN915736
Cathetus myrtifolius (2)	Bouman & Yong RWB053 (HITBC)	MN915996	MN904371	MN915496	MN916215	MN915737
Cathetus myrtifolius (3)	Yu 58 (L)	MN915997	MN904372		MN916216	MN915738
*Cathetus patentipilis**	Bruhl 1810 (NE)	MN916020	MN904392	MN915518	MN916234	MN915759
Cathetus petraeus	Blyden 1037 (WAG)	MN916026	MN904397	MN915524	MN916239	MN915763
Cathetus recurvatus	Wilson 612 (NE)	MN916046	MN904414	MN915543	MN916258	MN915778
Cathetus simplex (1)	Bouman RWB069 (L)	MN916074	MN904440	MN915572	MN916276	MN915805
Cathetus simplex (2)	Bouman RWB070 (L)	MN916075	MN904441	MN915573	MN916277	MN915806
Cathetus ussuriensis	Kawakita 124 (KYO)		FJ235366		FJ235274	
Cathetus virgatus	Wrigley & Telford 46642 (K)	AY936738	MN904442	MN915574	AY936639	MN915807
Cathetus welwitschianus	Bidgooet *et al.* 1882 (K)	AY936739			AY936640	
Cathetus wheeleri	Kathriarachchi *et al.* 33 (K)	AY936740	MN904445	MN915577	AY936641	MN915810
Cicca ambatovolanus	Randriamampionona *et al.* 51 (K)	MN915848	MN904218	MN915332	MN916115	MN915605
Cicca ankarana	Ralimanana *et al.* 663 (K)	MN915851	MN904221	MN915335	MN916118	MN915608
Cicca ankaratrae	Rakotonasolo & Zachary 802 (K)	MN915852	MN904222	MN915336	MN916119	MN915609
Cicca bernieranus	Phillipson 5373 (K)	MN915862	MN904232	MN915348	MN916128	MN915619
Cicca betsileanus	Labat 2402 (K)	MN915863	MN904233	MN915349	MN916360	MN915620

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Cicca chacoensis	Krapovickas *et al.* 45628 (K)	AY936677			AY936582	
Cicca cryptophila	Dumetz 593 (WAG)	MN915899	MN904265	MN915390	MN916358	MN915653
Cicca delpyana (1)	Kami 1215 (WAG)	MN915906		MN915397	MN916161	MN915659
Cicca delpyana (2)	M'Boungou 659 (WAG)		MN904272	MN915398	MN916160	
Cicca elsiae	Davidse & Gonzalez 13359 (L)	MN915916	MN904278	MN915408	MN916337	MN915667
Cicca engleri	Mwangulango 1138 (WAG)		MN905066	MN915410	MN916168	MN915669
Cicca humbertii	Kawakita 235 (KYO)		FJ235345		FJ235253	
Cicca kidna	Cheek 11531	FR715993			FR715992	
Cicca lichenisilvae	Antilahimena 7638 (MO)		MN904343	MN915464	MN916199	
Cicca mantadiensis (1)	Rasoazanany 110 (MO)	MN915979	MN904353	MN915479	MN916204	
Cicca mantadiensis (2)	Rasoazanany 514 (MO)	MN915980	MN904354	MN915480	MN916319	
Cicca marojejiensis	Kawakita 243 (KYO)		FJ235346		FJ235254	
Cicca oreichtitus	Antilahimena 4824 (MO)	MN916013	MN904385		MN916226	
Cicca perrieri	Rakotonasolo *et al.* 814 (K)	MN916024	MN904395	MN915522	MN916238	MN915762
Cicca philippioides	Ralimanana *et al.* 627 (K)	MN916027	MN904398	MN915525	MN916240	MN915764
Cicca physocarpa	McPherson 16148 (WAG)	MN916030	MN904401	MN915528	MN916243	MN915766
Cicca pinnata	Mav 1580 (K)	MN916032	MN904403	MN915530	MN916245	MN915704
Cicca polyantha	Breteler 1938 (WAG)	MN916033		MN915531	MN916246	MN915767
Cicca sambiranensis	Bürki *et al.* 3 (K)	MN916053	MN904421	MN915552	MN916315	MN915784
Cicca sp.	Ravelonarivo 3808 (MO)	MN915845	MN904295	MN915329	MN916282	
Moeroris vakinankaratrae	Ralimanana *et al.* 435 (K)	AY936737			AY936638	
Dendrophyllanthus aff. Comptonii	Munzinger 608 (MO)	MN915839	MN904214	MN915323	MN916111	
Dendrophyllanthus bourgeoisii	McMillan 5201 (WAG)	MN915870	MN905064	MN915357	MN916134	
Dendrophyllanthus bupleuroides	Mcpherson 18692 (MO)	MN915872	MN904237	MN915359	MN916136	
Dendrophyllanthus castus (1)	Mackee 16581 (L)	MN915879	MN904246	MN915367	MN916327	MN915632
Dendrophyllanthus castus (2)	Mcpherson 19255 (MO)	MN915880	MN904245	MN915368	MN916304	
Dendrophyllanthus caudatus	Kawakita 278 (KYO)		FJ235351		FJ235259	
Dendrophyllanthus chamaecerasus	Munzinger & McPherson 573 (MO)	AY936678			AY936583	
Dendrophyllanthus clamboides	Forster 26376 (L)	MN915893	MN904260	MN915382	MN916152	MN915646
Dendrophyllanthus cuscutiflorus	Yu 61 (L)	MN915901	MN904268	MN915392	MN916299	MN915654
Dendrophyllanthus dallachyanus	Forster 32938 (NE)			MN915393	MN916298	MN915655
Dendrophyllanthus dzumacensis	Jaffre 2412 (L)	MN915913	MN905065	MN915405	MN916164	MN915666
Dendrophyllanthus erwinii	Mitchell PRP1456 (NE)	MN915920	MN904281	MN915413	MN916338	
Dendrophyllanthus favieri	McPherson & Munzinger 18028 (MO)	AY936690			AY936596	
Dendrophyllanthus finschii	Takeuchi & Ama 15603 (L)	MN915924	MN904285	MN915416	MN916171	MN915674
Dendrophyllanthus guillauminii	Kawakita 273 (KYO)		FJ235353		FJ235261	
Dendrophyllanthus hypospodius	Bruhl *et al.* 1123 (L)		GQ503435	GQ503495	EU643744	GQ503559

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Dendrophyllanthus kanalensis	McPherson & Van der Werff 17886 (K)	AY936701			AY936604	
Dendrophyllanthus koniamboensis	Kawakita 277 (KYO)		FJ235350		FJ235258	
Dendrophyllanthus koumacensis	McPherson 19163A (MO)	MN915953	MN904331	MN915451	MN916191	
Dendrophyllanthus lacunarius	Bates 62700 (NE)	MN915955	MN904333	MN915453	MN916312	MN915706
Dendrophyllanthus lacunellus	Bates 62500 (NE)	MN915956	MN904334	MN915454	MN916313	MN915707
Dendrophyllanthus ligustrifolius (1)	McPherson 19091 (MO)	MN915965	MN904344	MN915465	MN916310	
Dendrophyllanthus ligustrifolius (2)	McPherson 5025 (L)	MN915966	MN904309	MN915466	MN916311	MN915714
Dendrophyllanthus loranthoides	MacKee 31810 (K)	AY936705			AY936607	
Dendrophyllanthus mangenotii	Kawakita 270 (KYO)		FJ235349		FJ235257	
Dendrophyllanthus panchierianus	McPherson & Munzinger 18264 (K)	AY936721	MN904391	MN915517	AY936623	MN915758
Dendrophyllanthus pilifer	McPherson 18525 (MO)	MN916031	MN904402	MN915529	MN916244	
Dendrophyllanthus poumensis	Mackee 20748 (L)	MN916039	MN904408	MN915537	MN916251	MN915772
Dendrophyllanthus sauropodoides	Forster 29857 (L)	EU623558	GQ503436	GQ503496	EU643745	GQ503560
Dendrophyllanthus serpentinus	Mackee 20770 (L)	MN916057		MN915556		MN915788
Dendrophyllanthus tenuirhachis	Yu & Tutie 165 (L)	MN916068	MN904435	MN915567	MN916271	MN915800
Dendrophyllanthus unifoliatus	Veillon 7986 (L)	AY936734			AY936635	
Dendrophyllanthus vulcani	Kawakita 274 (KYO)		FJ235354		FJ235262	
Emblica sp.	Yu 250 (L)	MN915889	MN904253	MN915377	MN916148	MN915640
Emblica pachyphylla (1)	Yahara *et al.* V3843 (L)	MN915853	MN904223	MN915337	MN916120	
Emblica pachyphylla (2)	Tagane *et al.* V3863 (L)	MN915854	MN904224	MN915338	MN916121	
Emblica bokorensis	Toyama *et al.* 1740 (FU)			MN915354	MN916132	
Emblica collinsae	Middleton 3302 (L)	MN915896	MN904263	MN915385	MN916155	MN915649
Emblica columnaris (1)	Fujikawa *et al.* 095327 (L)		MN904302	MN915387	MN916157	MN915651
Emblica columnaris (2)	Funakoshi *et al.* 085264 (L)	MN915897		MN915388	MN916283	MN915652
Emblica geoffrayi	Larsen *et al.* 3259 (L)	MN915936	MN904315	MN915430	MN935816	MN915685
Emblica officinalis (1)	Makino banical garden expedition(2015) 103008	MN915917	MN904279	MN915409	MN916167	MN915668
Emblica officinalis (2)	van Welzen 2003-11 (L)	GQ503378	GQ503434	GQ503494	EU643743	GQ503558
Emblica oxyphylla (1)	Middleton 3191 (L)	MN916018	MN904388	MN915515	MN916232	MN915755
Emblica oxyphylla (2)	Yu 174 (L)	MN916019	MN904389		MN916233	MN915756
Emblica pectinata	Yu 65 (L)	MN916022		MN915520	MN916236	MN915761
Emblica phuquocensis	Tagane *et al.* 5532 (FU)	MN916029	MN904400	MN915527	MN916242	
Emblica racemosa	Cooray 69090414 (L)	MN916035	MN904405	MN915533	MN916248	MN915769
Emblica rufuschaneyi	Van der Ent (L)		MN904418	MN915547	MN916259	MN915781
Emblica saffordii	Fosberg 59609 (L)	MN916050	MN904419	MN915549	MN916260	
Emblica urinaria (1)	Majaducon 5750 (L)	MN916071	MN904437	MN915569	MN916273	MN915802
Emblica urinaria (2)	Bouman RWB018 (L)	MN916072	MN904438	MN915570	MN916274	MN915803

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Flueggea acidoton	**S. Fuentes *et al.* 868 (B, HAJB)**	**LS975740**			**LS975798**	
Flueggea virosa (1)	Bouman & Yunhong RWB068 (HITBC)	MN915824	MN904197	MN915308	MN916091	
Flueggea virosa (2)	Mitchel 2890 (BRI)	MN915823			MN916104	
Flueggea virosa (3)	Chase 2104 (K)				AY552426	
Flueggea virosa (3)	Larsen *et al.* 45328 (L)		GQ503420	GQ503481		
Flueggea virosa (4)	Yu 64 (L)	MN915825	MN904198		MN916092	MN915588
Glochidion benthamianum	Bruhl 1026 (NE)	GQ503363		GQ503482		GQ503541
Glochidion carinatum	Toyama *et al.* 3212 (FU)		MN904243	MN915363	MN916138	
Glochidion ellipticum (1)	Bouman & Yong RWB058 (HITBC)	MN915826	MN904199	MN915310	MN916093	MN915589
Glochidion ellipticum (2)	Bouman & Yong RWB061 (HITBC)	MN915827	MN904200	MN915311	MN916094	MN915590
Glochidion ellipticum (3)	Bouman & Yong RWB062 (HITBC)	MN915829	MN904202	MN915309	MN916096	MN915591
Glochidion eriocarpum	Bouman *et al.* RWB027 (L)	MN915828	MN904201		MN916095	MN915592
Glochidion ferdinandi	Bruhl 2457 (NE)	GQ503366	GQ503421	GQ503484		GQ503543
Glochidion harveyanum	Bruhl 2527 (NE)	GQ503368	GQ503423	GQ503486		GQ503545
Glochidion kaweesakii	Pornpongrungrueng & Triyuttachai 1174 (KKU)	KY091120			KY091108	
Glochidion lanceolarium	Bouman & Yong RWB064 (HITBC)	MN915830	MN904203	MN915312	MN916097	MN915593
Glochidion lanceolatum	Kawakita 116 (KYO)	AY525687	FJ235327		FJ235235	
Glochidion lobocarpum	Bruhl 1146 (NE)	GQ503371	GQ503424	GQ503488		GQ503548
Glochidion mirabilis	Sirichamorn YSM 2009-05 (L)	HM132100	HM132101	HM132099		HM132102
Glochidion philippicum	Forster 29379 (NE)	GQ503373	GQ503426	GQ503490		GQ503550
Glochidion puberum	Chase 11460 (K)	AY936659			AY552428	
Glochidion roseum	Kawakita 143 (KYO)	KC913110	FJ235332		FJ235240	
Glochidion sphaerogynum (1)	Van der Scheur 128 (L)	MN915831	MN904204	MN915313	MN916280	MN915594
Glochidion sphaerogynum (2)	Van Welzen 2003-21 (L)	EU623555	GQ503427		EU643740	GQ503551
Glochidion wrightii	Bouman & Liu RWB032 (L)	MN915832	MN904205	MN915314	MN916098	MN915595
Heterosavia bahamensis	Wurdack D048 (US)	AY936749	AY830381		AY830284	
Kirganelia baccata	Mitchell PRP1514 (NE)			MN915342	MN916126	MN915613
Kirganelia castica	Wolhauser SW60172 (WAG)	MN915878	MN904244	MN915366	MN916141	
Kirganelia ciccoides	Paijmans 2876 (DAV)	MN915891			MN916150	
Kirganelia dinklagei (1)	Bissiengou (WAG)	MN915908	MN904273	MN915399	MN916333	MN915660
Kirganelia dinklagei (2)	Maas 9993 (WAG)	MN915909	MN904274	MN915400	MN916334	MN915661
Kirganelia flexuosa (1)	Chow 132 (L)	MN915927	MN904289	MN915419	MN916173	MN915677
Kirganelia flexuosa (2)	Mcnamara 162 Living collection Berkeley	MN915928	MN904290	MN915420	MN916174	MN915678
Kirganelia flexuosa (3)	Aung *et al.* 092433 (MBK)	MN915929	MN904288	MN915421	MN916172	MN915679
Kirganelia fuscolurida (1)	Dorr 3650 (WAG)	MN915933	MN905068	MN915425	MN916180	
Kirganelia fuscolurida (2)	Schatz 1737 (WAG)	MN915934	MN904296	MN915426	MN916179	
Kirganelia glauca	Bouman & Liu RWB028 (L)	MN915940	MN904291	MN915434	MN916175	MN915689
Kirganelia matitanensis	Ravelonarivo 4276 (MO)	MN915981	MN904355	MN915481	MN916205	

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Kirganelia microcarpa (1)	Bouman & Yong RWB056 (HITBC)	MN915985	MN904358	MN915483	MN916207	MN915729
Kirganelia microcarpa (2)	Yang *et al.* V2332 (L)	MN915986	MN904359	MN915484	MN916356	
Kirganelia microcarpa (3)	Tanaka *et al.* MY112 (L)	MN915987	MN904360	MN915485	MN916346	
Kirganelia microcarpa (4)	Yahara *et al.* 4346 (L)		MN904361	MN915486	MN916208	
Kirganelia muelleriana (1)	Kew Seed bank collection 145024	MN915991	MN904366	MN915491	MN916295	
Kirganelia muelleriana (2)	Bingham 6893 (WAG)	MN915992	MN904368	MN915492	MN916212	MN915734
Kirganelia muelleriana (3)	Jongkind 39824 (WAG)	MN915993	MN904367	MN915493	MN916211	MN915735
Kirganelia muelleriana (4)	Wieringa 7074 (WAG)	MN915994	MN904369	MN915494	MN916213	
Kirganelia novae-hollandiae	Telford 13024 (NE)	MN916001	MN904376	MN915500	MN916219	MN915741
Kirganelia oligosperma	Kawakita 101 (KYO)		FJ235360		FJ235268	
Kirganelia ovalifolia (1)	Mallaisse 12688 (WAG)	MN916014	MN904312	MN915512	MN916227	MN915751
Kirganelia ovalifolia (2)	de Wilde 7622 (WAG)	MN916015		MN915513	MN916228	MN915752
Kirganelia ovalifolia (3)	Friis 13337 (WAG)	MN916016	MN904301	MN915514	MN916229	MN915753
Kirganelia pervilleana (1)	Hoffmann *et al.* 392 (K)	AY936723			AY936625	
Kirganelia pervilleana (2)	Randrianasolo 526 (MO)	MN916025	MN904396	MN915523	MN916351	
Kirganelia polypserma (1)	Kew seed bank HBL20160135 (Kew seed bank 174282)	MN916037	MN904406	MN915535	MN916249	
Kirganelia polypserma (2)	Saolomao 40 (WAG)	MN916038	MN904407	MN915536	MN916250	MN915770
Kirganelia polypserma (3)	Friis 10341 (WAG)	MN916036	MN904386	MN915534	MN916230	MN915771
Kirganelia purpurea	Ward *et al.* 10442 (K)	MN916042	MN904411	MN915540	MN916254	MN915775
Leptopus chinensis	Brownless (L)	MN915833	MN904206	MN915315	MN916099	
Lingelsheimia sp.	Rabenantoandro *et al.* 1115 (MO)	AY936662	AY830375		AY830272	
Lysiandra calycina	Chase MWC 2163 (K)	AY936674	AY579869		AY552446	
Lysiandra carpentariae	Clarkson & Neldner 8410 (L)	MN915877	MN905063	MN915365	MN916140	MN915631
Lysiandra cauticola	Mitchell 837 (NE)	MN915881	MN904247	MN915369	MN916303	MN915633
Lysiandra cf. carpentariae	Hyland 8033 (L)	MN915888	MN904256	MN915376	MN916147	MN915639
Lysiandra collina	Telford & Bruhl 13119 (L)		MN904264	MN915386	MN916156	MN915650
Lysiandra flagellaris	Fryxell & Craven (L)	MN915926	MN904287	MN915418	MN916307	MN915676
Lysiandra fuernrohrii	Coveny 13478 (NE)		MN904294		MN916178	
Lysiandra grandisepala	Albrecht 13268 (NE)	MN915942	MN904319	MN915436	MN916289	MN915690
*Lysiandra graniticola**	Telford 13004 (NE)	MN915943	MN904320	MN915437	MN916185	MN915691
Lysiandra gunnii	Coveny 11474 (L)	MN915944	MN904322	MN915439	MN916290	MN915693
Lysiandra hebecarpa	Copeland NE66669 (NE)		MN904324		MN916308	MN915695
Lysiandra hirtella	Pedersen 1328 (L)	MN915947	MN904326	MN915442	MN916187	MN915697
Lysiandra microclada	Telford 13038 (L)	MN915988	MN904362	MN915487	MN916320	MN915730
Lysiandra mitchelii	Bruhl 1919B (NE)	MN915990	MN904365	MN915490	MN916210	MN915733
Lysiandra subcrenulata	Streimann s.n. (L)	MN916063	MN904432		MN916270	MN915795
Lysiandra trachygyne	Egan 2886 (NE)	MN916069	MN904436	MN915568	MN916294	MN915801

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Margaritaria anomala	Ramison 413 (MO)	MN915834			MN916100	
Margaritaria discoidea (1)	Nicholson 1 (L)		MN904208	MN915317	MN916102	
Margaritaria discoidea (2)	Nicholson s.n. (L)		MN904207	MN915316	MN916101	
Margaritaria dubiumtraceyi	Forster 29387 (BRI)			MN935815	MN916103	
Margaritaria indica	Orr 80532		MN904209	MN915318	MN916105	
Margaritaria nobilis	Orr 875422		MN904210	MN915319	MN916106	MN915596
Margaritaria rhomboidalis	Rabenantoandro *et al.* 656 (K)	AY936665			AY936571	
Margaritaria sp. Uganda	Nicholson 3a (L)	MN915835	MN904211	MN915320	MN916107	MN915597
Moeroris sp.	Ravelonarivo 4264 (MO)	MN915846		MN915330	MN916281	
Moeroris amara (1)	van Welzen 2006-5(L)	EU623557	GQ503433	GQ503493	EU643742	GQ503557
Moeroris amara (2)	Wieringa 8189 (WAG)	MN915847	MN904217	MN915331	MN916114	
Moeroris arenaria	Worthington 18323 (L)	AY936743	AY830380		AY830280	
Moeroris boehmii (1)	Gereau 5007 (WAG)	MN915864	MN904254	MN915350	MN916302	MN915621
Moeroris boehmii (2)	Wieringa 8841 (WAG)	MN915865	MN904234	MN915351	MN916129	MN915622
Moeroris boehmii (3)	Bidgood 6838 (WAG)	MN915866	MN904235	MN915352	MN916130	MN915623
Moeroris boehmii (4)	Lisowski 13765 (WAG)	MN915867	MN904303	MN915353	MN916131	MN915624
*Moeroris bongensis**	de Wilde 7858 (WAG)	MN915868	MN904305	MN915355	MN916284	
Moeroris caesiifolia	Cheek 10376 (WAG)	MN915875	MN904242	MN915362	MN916137	MN915629
Moeroris ceratostemon	Bidgood 6776 (WAG)	MN915882	MN904248	MN915370	MN916142	MN915634
Moeroris cf. boehmii	Friis 13159 (WAG)	MN915883	MN904249	MN915371	MN916143	MN915635
Moeroris cf. fischeri	de Wilde 4391 (WAG)	MN915887	MN905067	MN915375	MN916343	MN915725
Moeroris cf. rotundifolia	Nicholson 2 (L)		MN904329	MN915446	MN916342	MN915700
Moeroris coursii	Razafindrahaja 184 (MO)	MN915898	MN904266	MN915389	MN916329	
Moeroris debilis (1)	Bouman & Liu RWB037 (L)	MN915903	MN904269	MN915394	MN916330	MN915656
Moeroris debilis (2)	Bouman RWB071 (L)	MN915904	MN904270	MN915395	MN916331	MN915657
Moeroris debilis (3)	Kamarudim & Apok (L)	MN915905	MN904271	MN915396	MN916332	MN915658
Moeroris dimorpha	**E.R. Bcquer *et al.* HFC 87940 (HAJB)**	**LS975738**			**LS975795**	
Moeroris dinteri (1)	Dinter 213 (WAG)	MN915910		MN915401	MN916335	MN915662
Moeroris dinteri (2)	Oliver 6543 (WAG)	MN915911	MN905069	MN915402	MN916336	MN915663
Moeroris fischeri	Gereau 1996 (WAG)	MN915925	MN904286	MN915417		MN915675
Moeroris fraterna	Nooteboom 3010 (L)	MN915931		MN915423	MN916306	MN915681
Moeroris friesii	Harder *et al.* 2778 (WAG)	MN915932	MN904293	MN915424	MN916177	MN915682
Moeroris fuertesii	**S. Fuentes *et al.* 294 (B, HAJB)**	**LS975752**			**LS975812**	
Moeroris gabonensis (1)	Maas 10095 (WAG)		MN904299	MN915427	MN916181	MN915683
Moeroris gabonensis (2)	Wieringa 8492 (WAG)	MN915935	MN904313	MN915428	MN916182	
Moeroris gillettiana	Germishuizen 9727 (WAG)	MN915937	MN904316	MN915431		MN915686
Moeroris harrisii	Faulkner 3179 (WAG)	MN915945	MN904323	MN915440	MN916341	MN915694
Moeroris hutchinsoniana (1)	Poilecot 7974 (K)	AY936697	MN904327	MN915443	AY936601	MN915698
Moeroris hutchinsoniana (2)	Bamps 88 (WAG)	MN915948	MN904306	MN915444		
Moeroris kaessneri	Pocs 89182 (K)	AY936700			AY936603	
Moeroris leucantha (1)	de Wilde 4604 (WAG)	MN915962	MN904300	MN915460	MN916149	MN915642
Moeroris leucantha (2)	Friis 8619 (WAG)	MN915963	MN904340	MN915461	MN916344	MN915713

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Moeroris leucocalyx (1)	Bidgood 7161 (WAG)		MN904341	MN915462	MN916197	
Moeroris leucocalyx (2)	Bidgood 6969 (WAG)	MN915964	MN904342	MN915463	MN916198	
Moeroris limmuensis	de Wilde 6524 (WAG)	MN915967	MN904345	MN915467	MN916291	MN915715
Moeroris loandensis (1)	Pawek R597 (WAG)	MN915968	MN904346	MN915469	MN916201	MN915717
Moeroris loandensis (2)	Pawek 12535 (WAG)	MN915970	MN904297	MN915470	MN916202	MN915718
Moeroris loandensis (3)	Nuvunga 526 (WAG)	MN915969	MN905072	MN915471	MN916203	MN915719
Moeroris lokohensis	Antilahimena 8041 (MO)	MN915971	MN904347		MN916316	
Moeroris macrantha	Biegel *et al.* 4847 (WAG)	MN915972	MN905075	MN915472	MN916292	MN915720
Moeroris madagascariensis	McPherson 18925 (MO)	MN915973	MN904348	MN915473	MN916317	
Moeroris maderaspatensis	Hunter *et al.* 1532 (K)	AY936707			AY936609	
Moeroris magnificens	van der Burgt 1196 (WAG)	MN915975	MN904349	MN915475	MN916345	MN915722
Moeroris manniana (1)	Raynal 12256 (WAG)	MN915977	MN904351	MN915477	MN916347	MN915724
Moeroris manniana (2)	Biye 129 (WAG)	MN915978	MN904352	MN915478		MN915726
Moeroris melleri	Lowry *et al.* 5814 (K)	MN915983	MN904357	MN915482	MN916314	MN915728
Moeroris nirurioides (1)	Bidgood 8049 (WAG)	MN915998	MN904374	MN915497	MN916305	MN915739
Moeroris nirurioides (2)	Wieringa 7502 (WAG)	MN915999	MN904375	MN915498	MN916218	MN915740
Moeroris nummulariifolia (1)	Nicholson 3b (L)	MN916002	MN904377	MN915501	MN916288	MN915742
Moeroris nummulariifolia (2)	Wieringa 8374 (WAG)	MN916003	MN904380	MN915502	MN916361	MN915744
Moeroris nummulariifolia (3)	van Andel 5732 (WAG)	MN916004	MN904381	MN915503	MN916223	MN915743
Moeroris nummulariifolia (4)	Mwangoka 5900 (WAG)	MN916005	MN904379	MN915504	MN916222	
Moeroris nummulariifolia (5)	Razafitsalama 235 (MO)	MN916006	MN904378	MN915505	MN916220	
Moeroris nummulariifolia (6)	Blaxell 1118 (U)	MN916007	MN904310	MN915506	MN916221	MN915745
Moeroris nyale	Etuge 4453 (WAG)	MN916008	MN904382	MN915507	MN916224	MN915746
Moeroris odontadenia (1)	Darbyshire 207 (WAG)	MN916009	MN904311	MN915508	MN916348	MN915747
Moeroris odontadenia (2)	Bouman & Verwijs RWB025 (L)	MN916010	MN904383	MN915509	MN916349	MN915748
Moeroris odontadenia (3)	Wieringa 7665 (WAG)	MN916011	MN904384	MN915510	MN916350	MN915749
Moeroris oxycoccifolia	Gereau 5219 (WAG)	MN916017	MN904387		MN916231	MN915754
Moeroris paxii	Bidgood 2983 (WAG)	MN916021	MN904393	MN915519	MN916235	MN915760
Moeroris pentandra	Kew Seed bank collection 519962	MN916023	MN904394	MN915521	MN916237	
Moeroris phillyreifolia	van Nek 2188 (WAG)	MN916028	MN904399	MN915526	MN916241	MN915765
Moeroris procera (1)	**S. Fuentes *et al.* 428 (B, HAJB)**	**LS975737**			**LS975794**	
Moeroris procera (2)	**S. Fuentes *et al.* 414 (B, HAJB)**	**LS975769**			**LS975830**	
Moeroris rangoloakensis	Schatz *et al.* 3709 (K)	MN916045	MN904413	MN915542	MN916257	MN915777
Moeroris rheedii	Kathriarachchi *et al.* 1 (K)	AY936729	MN904415	MN915544	AY936630	MN915779
Moeroris rotundifolia	Wieringa 8849 (WAG)	MN916047	MN904416	MN915545	MN916352	MN915780
Moeroris sepialis	Luke 7112 (K)	AY936732			AY936633	
Moeroris stipulata (1)	Jansen-Jacobs 2813 (U)		MN904430	MN915561	MN916268	MN915793
Moeroris stipulata (2)	Gieteling 114 (WAG)	MN916062	MN904431	MN915562	MN916269	MN915794
Moeroris tenella (1)	Bruhl 2633 (L)	MN916065	MN904433	MN915564	MN916354	MN915797
Moeroris tenella (2)	Bouman RWB019 (L)	MN916066	MN904434	MN915565	MN916355	MN915798

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Moeroris tenella (3)	Groenendijk 15 (WAG)	MN916067	MN904308	MN915566	MN916357	MN915799
*Moeroris wakensis**	Wieringa 5107 (WAG)		MN904443	MN915575		MN915808
Nellica magudensis	Blokhuis 50 (WAG)	MN915976	MN904350	MN915476	MN916318	MN915723
Nellica mendoncae	de Wilde 6464 (WAG)	MN915984				
Nellica polygonoides	Kim & Miller 1078 (U)	MN916034	MN904404	MN915532	MN916247	MN915768
Notoleptopus decaisnei	Evans 3222 (K)	AM745836			AM745833	
Notoleptopus decaisnei	Fraser 267 (L)		GQ503431	GQ503491		GQ503555
Nymphanthus balgooyi (1)	Van der Ent	MN915857	MN904227	MN915343	MN916300	MN915614
Nymphanthus balgooyi (2)	Yu 192 (L)	MN915858	MN904228	MN915344	MN916301	MN915615
Nymphanthus balgooyi (3)	Yu 259 (L)	MN915859	MN904229	MN915345	MN916324	MN915616
Nymphanthus balgooyi (4)	Agoo 5700 (L)	MN915860	MN904230	MN915346	MN916325	MN915617
Nymphanthus buxifolius (1)	Yu 163 (L)	MN915873	MN904240	MN915360	MN916326	MN915627
Nymphanthus buxifolius (2)	Yu 167 (L)	MN915874	MN904241	MN915361	MN916285	MN915628
Nymphanthus cf. buxifolius (1)	Agoo 5659 (L)	MN915884	MN904238	MN915372	MN916286	MN915636
Nymphanthus cf. buxifolius (2)	Agoo 5683 (L)	MN915885	MN905070	MN915373	MN916287	MN915637
Nymphanthus cf. buxifolius (3)	Agoo 5738 (L)	MN915886	MN904239	MN915374	MN916328	MN915638
Nymphanthus cf. sootepensis	Bouman & Yong RWB059 (HITBC)	MN915890	MN904428	MN915378	MN916267	MN915643
Nymphanthus curranii	Yu 261 (L)	MN915900	MN904267	MN915391	MN916158	MN915604
Nymphanthus elegans (1)	Yahara *et al.* V3499 (L)	MN915914		MN915406	MN916165	
Nymphanthus elegans (2)	Yahara *et al.* V5597 (L)	MN915915	MN904277	MN915407	MN916166	
Nymphanthus floribundus	Kathriarachchi *et al.* 66 (K)	AY936682	MN904259	MN915381	AY936587	
Nymphanthus glaucescens (1)	Bouman & Yong RWB066 (HITBC)	MN916040	MN904409	MN915538	MN916252	MN915773
Nymphanthus glaucescens (2)	Esser 98-68 (L)	MN916041	MN904410	MN915539	MN916253	MN915774
Nymphanthus gomphocarpus	Klackenberg & Lundin 579 (L)	MN915941	MN905073	MN915435	MN916184	
Nymphanthus kinabalucius	Van der Ent (Kinabalu Parcs living collection)	MN915952	MN904330	MN915449	MN916190	MN915703
Nymphanthus laciniatus	Agoo 5660 (L)	MN915954	MN904332	MN915452	MN916192	MN915705
Nymphanthus leptoclados	Bouman & Yong RWB051 (HITBC)	MN915961	MN904339	MN915459	MN916196	MN915712
Nymphanthus longifolius	TRP-5004102 (BK)	AB550090				
Nymphanthus megalanthus	Calaramo (L)	MN915982	MN904356		MN916206	MN915727
Nymphanthus ruber	Lee *et al.* s.n. (CUHK)	AY765298				
Nymphanthus rubescens	Yahara *et al.* V2902 (L)	MN916048	MN904417	MN915546	MN916322	
Nymphanthus sootepensis (1)	Makino banical garden expedition(2015) 103251	MN916059	MN904426	MN915558	MN916297	MN915790
Nymphanthus sootepensis (2)	Makino banical garden expedition(2015) 103753	MN916060	MN904427	MN915559	MN916266	MN915791
Nymphanthus tetrandrus	Fujikawa *et al.* 053175 (L)	MN916058	MN904425	MN915557	MN916296	MN915789
Nymphanthus watsonii	Yu 225 (L)	MN916076	MN904444	MN915576	MN916278	MN915809

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Phyllanthus acidus	van welzen 2003-14(L)	MN915836	GQ503432	GQ503492	MN916108	GQ503556
Phyllanthus acuminatus (1)	Breteler 4238 (WAG)	MN915837	MN904212	MN915321	MN916109	MN915598
Phyllanthus acuminatus (2)	Wallnöfer 6031 (U)	MN915838	MN904213	MN915322	MN916110	MN915599
Phyllanthus aeneus	Kawakita 272 (KYO)		FJ235352		FJ235260	
Phyllanthus angustifolius	Lauerer 091479	MN915849	MN904219	MN915333	MN916116	MN915606
Phyllanthus anisolobus	Liesner 14363 (U)	MN915850	MN904220	MN915334	MN916117	MN915607
Phyllanthus arbuscula	Reynders19074182 (L)	MN915855	MN904226	MN915339	MN916123	MN915610
Phyllanthus arenicola	Maas & Carauta (U)		MN905071	MN915340	MN916124	MN915611
Phyllanthus attenuatus	Breteler 4696 (WAG)	MN915856	MN904304	MN915341	MN916125	MN915612
Phyllanthus botryanthus	de Wilde 31 (WAG)	MN915869	MN904255	MN915356	MN916133	MN915625
Phyllanthus brasiliensis	Ule 6408 (L)	MN915871	MN904236	MN915358	MN916135	MN915626
Phyllanthus caroliniensis	Groenendijk 55 (WAG)	MN915876		MN915364	MN916139	MN915630
Phyllanthus cf.klotzschianus	Carneiro 10 (K)			MN915450		MN915641
Phyllanthus chamaecristoid	van Ee *et al.* 404 (K)	AY936679			AY936584	
Phyllanthus chryseus	Van Ee *et al.* 387 (K)	AY936681	MN904257	MN915379	AY936586	MN915644
Phyllanthus cinctus	Ekman 19166 (K)	MN915892	MN904258	MN915380	MN916151	MN915645
Phyllanthus claussenii	Hatschbach 64117 (U)	MN915894	MN904261	MN915383	MN916153	MN915647
Phyllanthus comosus	Gutierrez *et al.* 81777 (WIS)	AY936685			AY936590	
Phyllanthus comosus (2)	**T. Borsch *et al.* 4271 (B, HAJB)**	**LS975727**			**LS975785**	
Phyllanthus dawsonii	da Silva 2073 (DAV)	MN915902			MN916159	
Phyllanthus dictyospermus	Santos 5712 (DAV)	MN915907			MN916162	
Phyllanthus discolor	Berazain *et al.* 71878 (K)	AY936688	MN904275	MN915403	AY936593	MN915664
Phyllanthus epiphyllanthus (1)	Lauerer 080405	MN915918	MN904225	MN915411	MN916122	MN915670
Phyllanthus epiphyllanthus (2)	Reynders IPEN:XX-0-BR-19840633 (L)	MN915919	MN904280	MN915412	MN916169	MN915671
Phyllanthus evanescens	Stevens 32461 (MO)	MN915921	MN904282	MN915414	MN916339	
Phyllanthus excisus	**W. Greuter *et al.* 28281 (B, HAJB, P-Gr)**	**LS975746**			**LS975806**	
Phyllanthus fluitans	Krämer xx-0-Dath-518 (L)	MN915930	MN904292	MN915422	MN916176	MN915680
Phyllanthus graveolens	Klitgaard *et al.* 399 (K)	AY936696	MN904321	MN915438	AY936600	MN915692
Phyllanthus heliotropus	Maas *et al.* 7762 (U)	MN915946	MN904325	MN915441	MN916186	MN915696
Phyllanthus incrustatus	**T. Borsch *et al.* 4504 (B, HAJB)**	**LS975731**			**LS975788**	
Phyllanthus juglandifolius	Bouman RWB16	MN915949	MN904328	MN915445	MN916188	MN915699
Phyllanthus klotzschianus	Grappo *et al.* 780 (K)	AY936702			AY936605	
Phyllanthus lamprophyllus (1)	Agoo 5592 (L)	MN915957	MN904335	MN915455	MN916193	MN915708
Phyllanthus lamprophyllus (2)	Telford & Bruhl 13049 (L)	MN915958	MN904336	MN915456	MN916194	MN915709
Phyllanthus lamprophyllus (3)	Telford & Bruhl 13051 (L)	MN915959	MN904337	MN915457	MN916195	MN915710
Phyllanthus lamprophyllus (4)	Yu 161 (L)	MN915960	MN904338	MN915458	MN916309	MN915711
Phyllanthus lindenianus	**S. Fuentes *et al.* 1003 (B)**	**LS975755**			**LS975815**	
Phyllanthus lindenianus	Fuertes 345 (K)			MN915468	MN916200	MN915716

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Phyllanthus madeirensis	Vincentini 1206 (U)	MN915974	MN905078	MN915474	MN916293	MN915721
Phyllanthus maleolens	**S. Fuentes *et al.* 1121 (B)**	**LS975756**			**LS975816**	
Phyllanthus microdictyis	Van Ee 399 (K)	AY936709	MN904363	MN915488	AY936612	MN915731
Phyllanthus mimosoides	Reynders 19074179 (L)	MN915989	MN904364	MN915489	MN916209	MN915732
Phyllanthus mirifcus	**T. Borsch *et al.* 5021 (B, HAJB)**	**LS975774**			**LS975835**	
Phyllanthus niruri	De la Quintana 333 (MO)	MN916000	MN904373	MN915499	MN916217	
Phyllanthus nummularioides	**S. Fuentes *et al.* 880 (B)**	**LS975753**			**LS975813**	
Phyllanthus nutans	**S. Fuentes *et al.* 996 (B)**	**LS975754**			**LS975814**	
Phyllanthus orbicularis	Eschevaria s.n. (L)	MN916012	MN904298	MN915511	MN916225	MN915750
Phyllanthus pachystylus	Van Ee 402 (K)	AY936720	MN904390	MN915516	AY936622	MN915757
Phyllanthus phlebocarpus	**P.A. Gonzalez HFC 87732 (HAJB)**	**LS975758**			**LS975819**	
Phyllanthus pseudocicca (1)	**B. Falcon *et al.* HFC 87780 (HAJB)**	**LS975736**			**LS975793**	
Phyllanthus pseudocicca (2)	**P.A. Gonzalez HFC 87681 (HAJB)**	**LS975759**			**LS975820**	
Phyllanthus purpusii	Breedlove 42730 Living collection Berkeley	MN916043	MN904412	MN915541	MN916255	MN915776
Phyllanthus ramillosus	Arbo 6945 (DAV)	MN916044			MN916256	
Phyllanthus ruscifolius	Cuatrecasas 21631 (U)	MN916049	MN905077	MN915548		MN915782
Phyllanthus salviifolius (1)	Balslev 1888 (U)	MN916051	MN905076	MN915550	MN916261	
Phyllanthus salviifolius (2)	Jorgensen 61204 (U)	MN916052	MN904420	MN915551	MN916262	MN915783
Phyllanthus sellowianus (1)	Chase 14776	MN916054	MN904422	MN915553	MN916263	MN915785
Phyllanthus sellowianus (2)	Chase 14777	MN916055	MN904423	MN915554	MN916264	MN915786
Phyllanthus sellowianus (3)	Chase 14463	MN916056	MN904424	MN915555	MN916265	MN915787
Phyllanthus sp. sect. Callitrichoides	**B. Falcon *et al.* HFC 87779 (HAJB)**	**LS975742**			**LS975801**	
Phyllanthus spruceanus	Maas & Maas 474 (U)	MN916061	MN904429	MN915560	MN916353	MN915792
Phyllanthus subcarnosus	**T. Borsch *et al.* 4707 (B, HAJB)**	**LS975741**			**LS975800**	
Phyllanthus symphoricarpoides	Cuatrecasas 18421 (U)	MN916064	MN904307	MN915563	MN916321	MN915796
Phyllanthus tuerckheinii	Mendez 8022 (DAV)	MN916070			MN916272	
Phyllanthus vacciniifolius	Hokche *et al.* 854 (U)	MN916073	MN904439	MN915571	MN916275	MN915804
Phyllanthus williamioides	**T. Borsch *et al.* 4523 (B, HAJB)**	**LS975730**			**LS975787**	
Phyllanthys myrtilloides subsp. Alainii	**S. Fuentes *et al.* 556 (B, HAJB)**				**LS975799**	
Phyllanthys myrtilloides subsp. Erythrinus	**W. Greuter *et al.* 28014 (B, HAJB, P-Gr)**	**LS975734**			**LS975791**	
Phyllanthys myrtilloides subsp. Shaferi	**S. Fuentes *et al.* 426 (B, HAJB)**	**LS975743**			**LS975802**	
Phyllanthys myrtilloides subsp. Spathulifolius	**P.A. Gonzalez HFC 87731 (HAJB)**	**LS975772**			**LS975833**	
Plagiocladus diandrus	Wieringa 2903 (WAG)				AY936592	
Plagiocladus diandrus	de Wilde & de Wilde 11641 (WAG)	AY936687				
Synostemon albiflorus (1)	Forster 32329 (NE)	MN916077	MN904446	MN915578	MN916279	MN915811

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Appendix 2. (Continued)

Matrix name	Voucher	ITS	PHYC	*accD-psaI*	*matK*	*trnS-trnG*
Synostemon albiflorus (2)	Forster 34400 (NE)	MN916078	MN904447	MN915579	MN916323	MN915812
Synostemon bacciformis	Cowie I 3418 (L)	GQ503382		GQ503502		
Synostemon bacciformis	Kerr 8350 (L)				EU643753	
Synostemon bacciformis	Pruesapan 2009-4 (L)		GQ503440			
Synostemon hirtellus	Bean 15558 (BRI)	EU623573	GQ503447	GQ503508	EU643763	GQ503574
Synostemon kakadu	Bruhl 1270 (NE)	GQ503395	GQ503451	GQ503510		GQ503578
Synostemon sphenophyllus	Gray 08597 (BRI)	GQ503402	GQ503465		EU643780	GQ503597
Synostemon spinosus	Bean 20738 (NE)	GQ503403	GQ503466	GQ503524		GQ503598
Synostemon trachyspermus	Bell 547 (NE)	GQ503407	GQ503470	GQ503528	EU643784	GQ503602

Supplementary figure 1. Phylogeny of tribe Phyllantheae from combined dataset of Bouman *et al.* (2021) and Falcón *et al.* (2020) showing the new classification proposed here; clade labels A-I follow figure 1. Dataset is composed of nuclear (ITS and *PHYC*) and plastid (*accD–psaI*, *matK* and *trnS–trnG*) markers. Posterior probabilities (PP) from Bayesian inference are displayed above nodes; Maximum Likelihood bootstrap scores are displayed below the nodes. Undescribed species are indicated with an asterisk (*).