



Universiteit
Leiden
The Netherlands

A revised phylogenetic classification of tribe Phyllanthaeae (Phyllanthaceae)

Bouman, R.W.; Kessler, P.J.A.; Telford, I.R.H.; Bruhl, J.J.; Strijk, J.S.; Saunders, R.M.K.; ... ;
Welzen, P.C. van

Citation

Bouman, R. W., Kessler, P. J. A., Telford, I. R. H., Bruhl, J. J., Strijk, J. S., Saunders, R. M. K., ... Welzen, P. C. van. (2022). A revised phylogenetic classification of tribe Phyllanthaeae (Phyllanthaceae). *Phytotaxa*, 540(1), 1-100. doi:10.11646/phytotaxa.540.1.1

Version: Publisher's Version

License: [Leiden University Non-exclusive license](#)

Downloaded from: <https://hdl.handle.net/1887/3281151>

Note: To cite this publication please use the final published version (if applicable).



PHYTOTAXA

540

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, Universidad 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



Magnolia Press
Auckland, New Zealand

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

A revised phylogenetic classification of tribe Phyllanthae (Phyllanthaceae)

(*Phytotaxa* 540)

100 pp.; 30 cm.

18 March 2022

ISBN 978-1-77688-486-5 (paperback)

ISBN 978-1-77688-487-2 (Online edition)

FIRST PUBLISHED IN 2022 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

<https://www.mapress.com/pt/>

© 2022 Magnolia Press

All rights reserved.

No part of this publication may be reproduced, stored, transmitted or disseminated, in any form, or by any means, without prior written permission from the publisher, to whom all requests to reproduce copyright material should be directed in writing.

This authorization does not extend to any other kind of copying, by any means, in any form, and for any purpose other than private research use.

ISSN 1179-3155 (print edition)

ISSN 1179-3163 (online edition)

Abstract

The majority of tribe Phyllanthae (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 Phyllanthae will consist of the following 18 genera: *Breynia*, *Cathetus*, *Cicca*, *Dendrophyllanthus*, *Embllica*, *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 Phyllanthae: *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 Phyllanthae with global distribution and (estimated) number of species for each group.

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

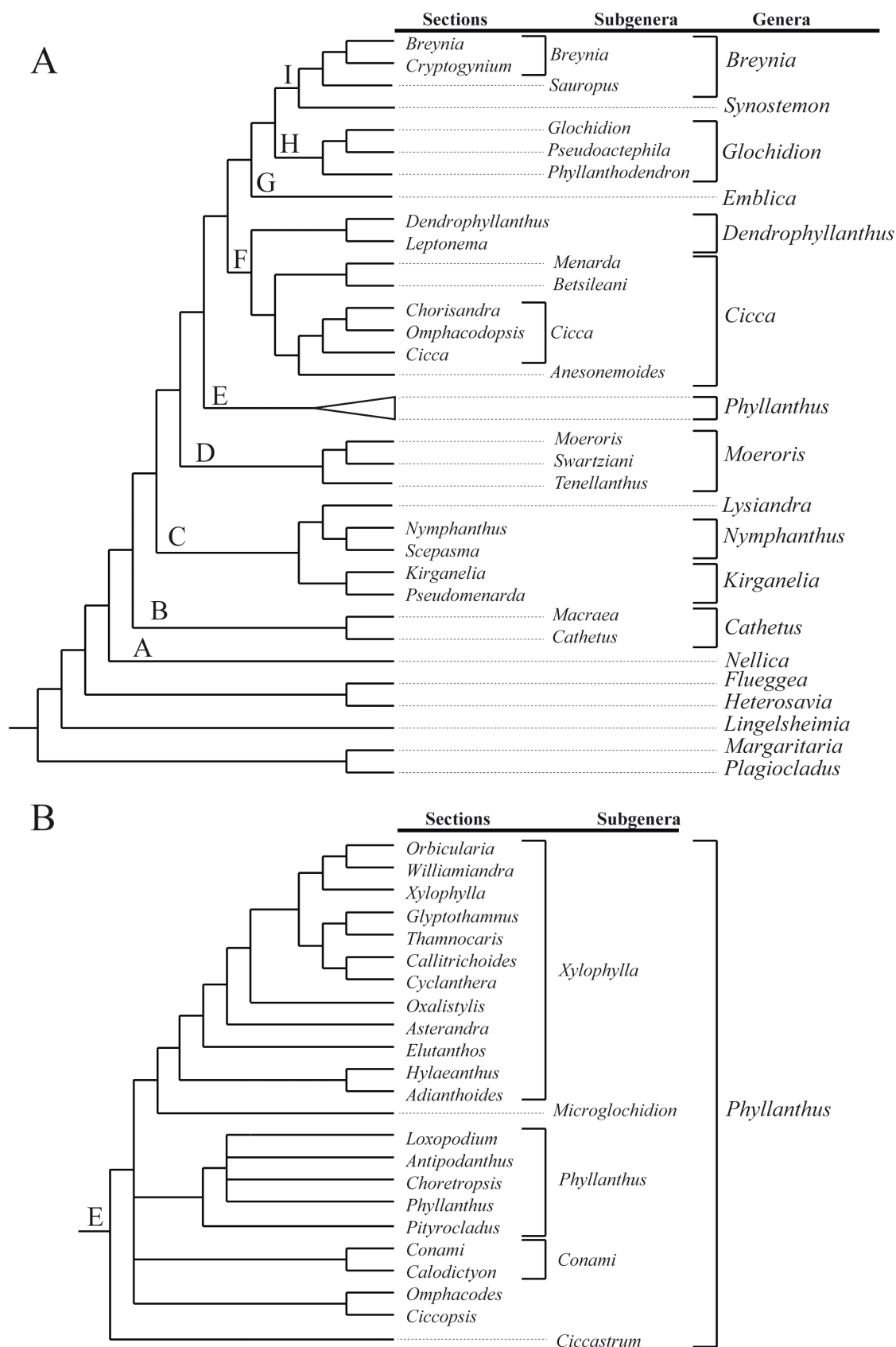


FIGURE 1. (A) Summary phylogeny showing relations between genera in tribe Phyllanthae from Bayesian and Maximum Likelihood analysis of five markers (ITS, *PHYC*, *accD-psaI*, *trnS-trnG*, *matK*), modified from Appendix 1. Classification is shown of genera (right column), subgenera (middle column) and 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.

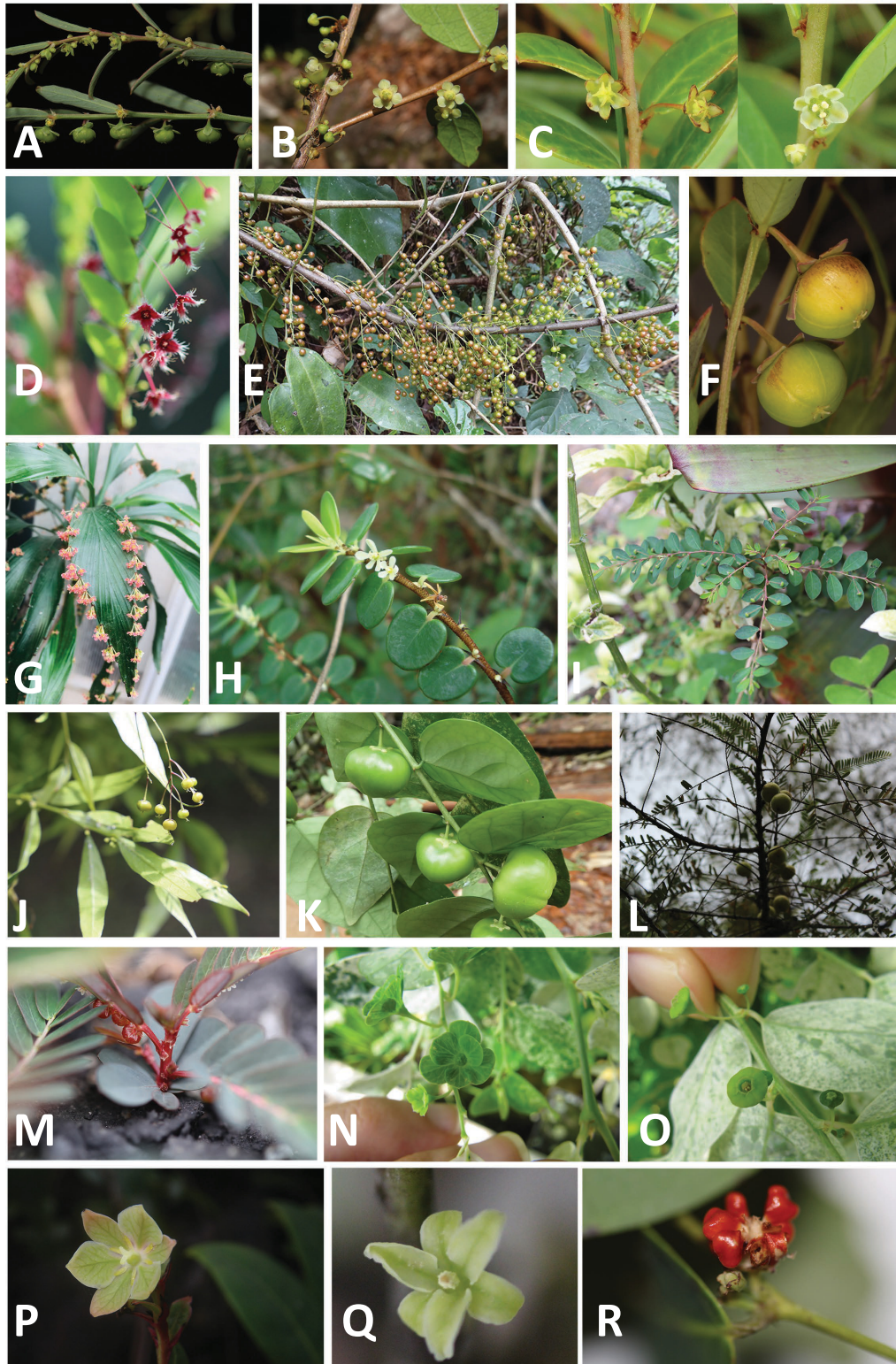


FIGURE 2. Images of representative members of tribe Phyllanthae. (A) Flowers of *Nellica maderaspatensis*. (B) Pistillate flowers of *Cathetus gracilis*, note the unique disc covering the ovary. (C) Pistillate and staminate flowers of *Cathetus glaucophyllus*. (D) Staminate flowers of *Nymphanthus glaucescens*. (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 Phyllanthaeae

With the following key the genera of tribe Phyllanthaeae 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 | <i>Lingelsheimia</i> |
| 2. | Stamens 4–7 | 3 |
| 3. | Branching non-phyllanthoid (laminar 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, laminar leaves and flowers on lateral axes, lateral branchlets deciduous); staminate sepals 4, stamens 4, filaments connate, anther connectives apiculate; fruits capsules—Asia | <i>Glochidion</i> (<i>G. moi</i>) |

| | | |
|------|---|---|
| 4. | Petals absent; fruits with 2 seeds per locule; pollen exine verruculose—Pantropical | <i>Flueggea</i> |
| 4. | Petals present; fruits with 1 or 2 seeds per locule; pollen exine reticulate—West Indies | <i>Heterosavia</i> |
| 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 <i>Cicca</i> section <i>Cicca</i> |
| 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 | <i>Dendrophyllanthus</i> |
| 8. | Staminate sepals often recurved; disc absent; filaments tightly together (separating as flowers age); ovary 3–15-locular—Australia, mainland Asia, Malesia, Pacific | <i>Glochidion</i> |
| 9. | Sepal scales often present in staminate flowers; fruits wider than long; seeds smooth | <i>Breynia</i> |
| 9. | Sepal scales absent in staminate flowers (except in <i>Synostemon bacciformis</i>); fruits longer than wide; seeds sculptured | <i>Synostemon</i> |
| 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 | <i>Lingelsheimia</i> |
| 11. | Stamens 2–5 | 12 |
| 12. | Sepals 4; staminate disc entire; stamens 4, filaments free; seeds with blue sarcotesta—Pantropical | <i>Margaritaria</i> |
| 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 <i>Moeroris arenaria</i>) | 14 |
| 13. | Staminate disc segmented into glands | 15 |
| 14*. | Sepals 6 in both sexes; staminate disc urceolate; stamens 3, filaments connate—Asia | <i>Cathetus</i> |
| 14*. | Sepals 6 in both sexes; staminate disc not urceolate; stamens 2, filaments free—Africa | <i>Plagiocladus</i> |
| 14*. | Sepals 4 in staminate flowers, 6 in pistillate flowers; staminate disc H-shaped around filaments; stamens 2, filaments free—North America | <i>Moeroris</i> (<i>M. arenaria</i>) |
| 15. | Sepals 5; stamens 5, filaments free—Africa | <i>Kirganelia</i> subgenus <i>Kirganelia</i> section <i>Pseudomenarda</i> |
| 15. | Sepals 5 or 6; stamens usually 3 (rarely 2), filaments connate (free in <i>Moeroris rosmarinifolius</i>)—Africa to Asia | 16 |
| 16. | Plagiotropic branchlets caducous, usually fascicled (non-phyllanthoid in section <i>Elutanthos</i> , but then with paniculate inflorescences); fruits capsules or berries | <i>Phyllanthus</i> |
| 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) | <i>Nellica</i> |
| 17. | Leaves on all axes distichous (except at basal nodes in <i>Cicca</i>); 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 | <i>Phyllanthus</i> subgenus <i>Phyllanthus</i> section <i>Loxopodium</i> |
| 18*. | Leaves distichous; pollen clypeate; seeds smooth or verrucate—Africa, Asia, Australia and Pacific | <i>Cathetus</i> subgenus <i>Macraea</i> |
| 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 | <i>Cicca</i> subgenus <i>Betsileani</i> |
| 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 dehiscent 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 dehiscent 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 dehiscent 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 dehiscent horizontally (*Nymphanthus* or *Phyllanthus chryseus*) or vertically (*Phyllanthus* section *Thamnocariss*)—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 dehiscent mostly vertically, sometimes horizontally 27
26. Inflorescences mostly unisexual; staminate disc segmented; anthers dehiscent 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 dehiscent horizontally (*P. chryseus*) or vertically (*P.* section *Thamnocariss*); 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, pinnatifid; stamens 3, filaments connate, anthers dehiscent vertically, connectives apiculate; pistillate disc segmented—Asia & Pacific *Glochidion*
28. Plagiotropic branchlets not differentiated and all with leaves of similar size (or unifoliate), sometimes bipinnatifid; stamens 3–20, filaments connate or free, anthers dehiscent horizontally to vertically, connectives apiculate or not; pistillate disc entire..29
29. Branchlets (bi-)pinnatifid; sepals often biseriolate (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 pinnatifid; 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 dehiscent 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 dehiscent horizontally (vertically 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 dehiscent 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 dehiscent 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 dehiscent 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 Phyllanthaceae 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 (laminar leaves and flowers on all axes; branchlets not deciduous).....2
1. Branching phyllanthoid (leaves on main stem reduced to scales, the cataphylls; laminar 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 flowers4
4. Leaves on all axes spirally arranged.....5
4. Leaves on all axes distichous6
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 sarcotesta7
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 sets10
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 (laminar 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; laminar leaves and flowers on lateral axes; lateral branchlets caducous)7
2. Disc absent..... *Synostemon*
2. Disc present3
3. Pistillode present in staminate flowers *Flueggea*
3. Pistillode absent in staminate flowers4

| | | |
|------|--|--|
| 4. | Leaves on all axes spirally arranged; filaments connate; pistillate disc segmented..... | <i>Nellica</i> |
| 4. | Leaves on all axes distichous; filaments free or connate; pistillate disc usually entire (when segmented then filaments free, except in <i>Cathetus womerleyi</i> and <i>Cathetus ussuriensis</i>)..... | 5 |
| 5. | Sepals 4 in both sexes; staminate disc entire; stamens 4, filaments free; seeds with blue sarcotesta | <i>Margaritaria</i> |
| 5. | Sepals 5 or 6 (4 in staminate flowers of <i>Cathetus ussuriensis</i> , but then only 2 stamens in staminate flowers and 6 sepals in pistillate flowers); staminate disc segmented (urceolate in <i>Cathetus gracilis</i> (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 | <i>Cathetus</i> |
| 6. | Branchlets caducous; stipule base truncate; filaments free, anther connective often enlarged; seeds smooth or transversely striate. | <i>Lysiandra</i> |
| 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 | <i>Dendrophyllanthus</i> |
| 9. | Staminate sepals often recurved; filaments connate; ovary 3–15-locular..... | <i>Glochidion</i> |
| 10. | Sepal scales often present in staminate flowers; fruits wider than long; seeds smooth | <i>Breynia</i> |
| 10. | Sepal scales absent in staminate flowers (except in <i>S. bacciformis</i>); fruits longer than wide; seeds sculptured | <i>Synostemon</i> |
| 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 | <i>Emblica</i> |
| 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 | <i>Moeroris</i> |
| 13. | Cataphyllary stipules not auriculate; filaments free | <i>Phyllanthus</i> |
| 14. | Sepals 4 in staminate flowers; stamens 2, filaments connate, anthers dehiscing horizontally (except in <i>Nym. ruber</i> & <i>Nym. touranensis</i>)—pollen pantoporate or clypeate..... | <i>Nymphanthus</i> |
| 14. | Sepals 5 or 6 in staminate flowers (4 in <i>Cicca acida</i> , 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..... | <i>Kirganelia</i> |
| 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 <i>Cicca pinnata</i> and <i>C. orientalis</i> , but then stamens 6).. .. | 16 |
| 16*. | Branchlets pinnatifid; inflorescences axillary or on separate leafless plagiotropic axes; stamens 4 (in <i>C. acida</i>) or 6 (in <i>C. Pinnata</i> and <i>C. orientalis</i>), filaments free; fruits baccate (spherical <2 cm in diam. in <i>C. pinnata</i> and <i>C. orientalis</i> ; star-shaped in <i>C. accida</i>) | <i>Cicca</i> |
| 16*. | Branchlets (bi-)pinnatifid; 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 | <i>Dendrophyllanthus</i> |
| 16*. | Branchlets pinnatifid; 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 <i>Emblica officinalis</i> , there spherical drupe 2–3 cm in diam.) | 17 |
| 17. | (Climbing) shrubs to trees; floriferous branchlets sometimes with smaller leaves, <i>Glochidion</i> subg. <i>Phyllanthodendron</i>); stamens 3 or 4, connectives apiculate; pistillate disc segmented, segments linear; fruits (inflated) capsules | <i>Glochidion</i> (subgenera <i>Phyllanthodendron</i> & <i>Pseudoactephila</i>) |
| 17. | Shrubs to trees; all branches with same size of leaves; stamens 3, connectives apiculate or not; pistillate disc entire; fruits capsules (drupaceous in <i>Emblica officinalis</i>)..... | 18 |
| 18. | Sepals 6; anthers dehiscing vertically, connectives often apiculate; fruits capsules (drupaceous in <i>E. officinalis</i>)..... | <i>Emblica</i> |
| 18. | Sepals 5 or 6; anthers dehiscing obliquely to horizontally, connectives not apiculate; fruits capsules..... | <i>Moeroris</i> |

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

1. Branching non-phyllanthoid (lamine 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 flowers3
2. Pistillode absent in staminate flowers4
3. Petals absent; fruits with 2 seeds per locule; pollen exine verruculose *Flueggea*
3. Petals present; fruits with 1 or 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 sarcotesta5
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 subshrubs7
6. Shrubs to trees, rarely climbers12
7. Inflorescences unisexual8
7. Inflorescences bisexual11
8. Pistillate inflorescences on proximal position and staminate inflorescences on distal position of plagiotropic branchlets; seeds transversely ribbed—ovary often covered with tubercles *Embllica 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 ribbed9
9. Cataphyllary stipules not auriculate *Phyllanthus*
9. Cataphyllary stipules (unilaterally) auriculate10
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) Nuttall (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 & Hoffmann (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 shrubs, 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 apically 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. Johnston.
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. Johnston.
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 (Müller 1866: 366) R.W. Bouman, *comb. nov.* Basionym: *Phyllanthus liebmannianus* Müll. Arg.
Nellica maderaspatensis (Linnaeus 1753: 982) Raf. (1838: 92, as '*maderaspatana*'). Basionym: *Phyllanthus maderaspatensis* 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 (Brandege 1899: 8) R.W. Bouman, *comb. nov.* Basionym: *Phyllanthus peninsularis* Brandege.
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 (Benth 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 Shaw 1971: 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 pinnatifid, 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 aberrant 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 & Hoffmann (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 pinnatifid, 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 mucicous, 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.* (2020) 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 Benth 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 fuscolorida (Müller 1866: 346) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fuscoloridus* 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 (Benth 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* Schumacher & Thonn.

Kirganelia reticulata (Poir 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 (Benth 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 (Benth 1873: 106) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus flagellaris* Benth.
Lysiandra fuernrohrrii (Mueller 1855: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fuernrohrrii* 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 (Benth 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 michellii* Benth (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 pinnatifid. *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, Malasia.

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 *Embliscastrum* 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-Smitih 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).—*Epistylum* 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 pinnatifid. *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 Pfeiffer (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 (Benth 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 tetrandrus* 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* (Pornpongrueng, Parnell & Hodkinson in Pornpongrueng *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 fimbriicalyx* (Li 1987a: 380) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fimbriicalyx* 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* (Pornpongrueng, Chantaranotha & J.Parnell in Pornpongrueng *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 kampoensis* (Beille 1927: 606) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kampoensis* 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 leptocladus* (Benth 1861: 312) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leptocladus* Benth.
- Nymphanthus leytensis* (Elmer 1908: 307) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus leytensis* Elmer.
- Nymphanthus liukuensis* (Matsumura ex Hayata 1904: 11) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus liukuensis* 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: *Epistylum 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 *Embliscastrum* Müller (1866: 324).—*Glochidion* J.R.Forst. & G.Forst. section *Embliscastrum* (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 pinnatifid. *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 pinnatifid (rarely bi-pinnatifid 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 *Emblia* (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 pinnatifid. *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, perihexabreviusulcate or sulcate macro- or biretulate, 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 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 volkensisii* (Engler 1895: 236) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus volkensisii* 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.
- Reverchonnia* Gray (1880: 107); Pax & Hoffmann (1931: 66); Webster & Miller (1963: 200); Webster (1994: 45).—*Phyllanthus* L. section *Reverchonnia* (A.Gray) Webster (2007: 235).—Type: *Reverchonnia arenaria* A.Gray (= formerly *Phyllanthus warnockii* G.L.Webster) = *Moeroris arenaria* (A.Gray) R.W.Bouman.

Diagnostic features: Herbs, monoecious, branching phyllanthoid with pinnatifid 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*) originally 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)pinnatifid. *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)pinnatifid, 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 (lamine 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, punctulate, 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* Steyerem. (Steyermark *et al.* 1952: 321) and *P. bolivarensis* Steyerem. (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 specific 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* Steyerem., *P. harrimani* Webster (1978: 570), *P. hortensis* Govaerts & Radcliffe-Smith (1996: 177), *P. lasiogynus* Müller (1866: 357), *P. orinocensis* Steyerem., *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 pinnatifid. *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 pinnatifid. *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 pinnatifid. *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, dehiscent 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* Brandege (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)pinnatifid (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 dehiscent ± 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 pinnatifid. *Brachyblasts* absent. *Cataphylls* oblong-elliptic, membranous. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 6, whorls indistinct; disc glands 6; stamens 3, filaments free; anthers emarginate, dehiscent 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 indistinct. *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 pinnatifid. *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 bipinnatifid. *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 punctulate.

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. anisobolus* Müller (1866: 382), *P. brasiliensis* (Aublet 1775: 926) Poirlet (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 *Francaavillani* Brunel (1987: 236).—Type: *Phyllanthus francaavillanus* Beille (= *Phyllanthus myrsinites* Kunth subsp. *francaavillanus* (Müll.Arg.) G.L.Webster)

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatifid. *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, dehiscent 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 *Francaavillanus* 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. francaavillanus* 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 *Francaavillani* might have to be reversed in the future. Both groups agree in general floral morphology, although Brunel (1987) did describe the pollen of section *Francaavillani* 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. juaensis* 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 pinnatifid 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, dehiscent 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* Steyererm.), 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 pinnatifid and modified into flattened phylloclades, sometimes bipinnatifid. *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 synonymized 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. gladius* 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. (= *Phyllanthus 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* Brandege (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 pinnatifid. *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 usually 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 pinnatifid. *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 clausenii* Müll.Arg.

Diagnostic features: Subshrubs or shrubs, monoecious or dioecious, branching (often sub-) phyllanthoid, pinnatifid (sometimes bipinnatifid in *P. submarginatus*). *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 verrucae in lines.

Distribution: Tropical South America.

Included species (21 spp.): *P. acutifolius* Poir. 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. clausenii* 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. submarginatus* 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 pinnatifid. *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 autonoms 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 pinnatifid. *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).—*Phyllanthus* 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)pinnatifid, 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 pinnatifid, 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. Jablonski 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 bipinnatifid 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 pinnatifid, 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 pinnatifid 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 *Phyllanthus* 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 pinnatifid (sometimes bipinnatifid). *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. berterioanus* 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 pinnatifid. *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* Brandegees (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 **Epistylum** (Sw.) Griseb.

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

Phyllanthus L. section *Catastylum* 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 pinnatifid, 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 pinnatifid. *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 pinnatifid (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 pinnatifid. *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*, punctulate 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 **Oxalistrylis** Baill.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Oxalistrylis* 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 pinnatifid. *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 exerted 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 pinnatifid. *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 *Thamnocharis*, 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 pinnatifid, 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 dehiscent, 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 pinnatifid, 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, dehiscent 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 pinnatifid, 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), dehiscent 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)pinnatifid 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, obovate, 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 bipinnatifid 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* (Linnaeus 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* Poir (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.

Tricarum de Loureiro (1790: 557).—Type: *Tricarum cochinchinense* Lour. (= formerly synonym of *Phyllanthus acidus* (L.) Skeels) = *Cicca acida* (L.) Merr.

Staurothyra 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)pinnatifid (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 *Emblia* 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)pinnatifid. *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* Leandri.
- 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 pinnatifid, 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*, *Emblia* 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 pinnatifid. *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 pinnatifid. *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 *Polyanthis* Brunel (1987: 283).—Type: *Phyllanthus polyanthus* Pax = *Cicca polyantha* (Pax) R.W.Bouman.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatifid, 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-triangular, reniform or rounded, smooth or with minute striae.

Distribution: Africa.

Note—Section *Omphacodopsis* was found to be nested within section *Polyanthis* (Bouman *et al.* 2020; supplementary fig. 1). Sections *Omphacodopsis* and *Polyanthis* were originally distinguished based on differences in fruit (berry versus inflated capsule) and seed shape (reniform versus rounded). To prevent paraphyly of section *Polyanthis*, 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 pinnatifid (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 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)pinnatifid, 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 faguettii* Baill. = *Dendrophyllanthus faguettii* (Baill.) R.W.Bouman.

Leichhardtia Mueller (1876: 67), *nom. illeg.*, non *Leichhardtia* 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.

Nymanina Schumann (1905: 291), *nom. illeg.*, non *Nymanina* Lindberg (1868: 290).—*Phyllanthus* L. subgenus *Gomphidium* (Baill.) G.L.Webster section *Nymanina* (K.Schum.) Smith (1912: 781).—Type: *Nymanina 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)pinnatifid, 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 *Nymanina* (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 *Nymanina* (e.g. *D. tenuirhachis* (J.J.Sm.) R.W.Bouman: free; and *D. cuscutiflorus* (S.Moore) R.W.Bouman: connate). Bipinnatifid 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 *Embllica* (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 faguettii (Baillon 1862b: 237) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus faguettii* 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 sylvicola* S.Moore = *Dendrophyllanthus sylvicolus* (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 pinnatifid, 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 disc 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 meuiensis* (Schmid 1991: 249) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus meuiensis* 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 1980: 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 sylvicola (Moore 1921: 401) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sylvicola* 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 unifolius (Schmid 1991: 198) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus unifolius* 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 yvetteae (Schmid 1991: 309) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus yvetteae* 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 baeobotryoides* (Wall. ex Müll.Arg.) R.W.Bouman.

Diagnostic features: Herbs, shrubs or trees, monoecious, branching phyllanthoid, branchlets pinnatifid. *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-breviculcate, 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 *Benguensis*), 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 (Balakrishnan & 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* (Müller 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 benguensis (Robinson 1909: 78) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus benguensis* 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* Poirlet (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 & Hemsley.

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 erythrocooccus* 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 pinnatifid, 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 pinnatifid, 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 kanehirae* (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 multilobus* (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 anthopotanicum* (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 pinnatifid, 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 pinnatifid, 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 pinnatifid. *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 pinnatifid. *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 pinnatifid. *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.Balacr.

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatifid. *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 pinnatifid. *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 pinnatifid. *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*).

Acknowledgements

This work was carried out as part of the Ph.D. research of the first author, funded by the Hortus botanicus Leiden and Leiden University. The second author thanks the Leiden University Fund (LUF) for their support of the chair 'Botanical Gardens and Botany of Southeast Asia'. The last author thanks the Treub Maatschappij, the Society for the Advancement of Research in the Tropics, for their support of the Ornstein chair in Tropical Plant Biogeography. Royal Botanic Gardens Kew (K), Naturalis Biodiversity Center (L, U, WAG), Missouri Botanical Garden (MO) and the Muséum National d'Histoire Naturelle (P) are gratefully acknowledged for lending us material or sending us scans of herbarium material. Two anonymous reviewers are thanked for their comments to help improve our manuscript. Photographs were kindly supplied by several contributors and the authors wish to thank T. Williams of the Société des

Mines de Fer de Guinée, C. Jongkind, R.-Y. Yu and M.S. Nuraliev (whose photos were made during expeditions of the Joint Russian-Vietnamese Tropical Scientific and Technological Center).

References

- Adanson, M. (1763) *Familles des Plantes* 2. Vincent, Paris, pp. 1–640.
- Adelbert, A.G.L. & Meeuse, A.D.J. (1945) Euphorbiaceae. In: Backer, C.A.P.: Notes on the flora of Java, II. *Blumea* 5: 507–508.
- Airy Shaw, H.K. (1960) Notes on Malaysian Euphorbiaceae. *Kew Bulletin* 14: 469–471.
<https://doi.org/10.2307/4114765>
- Airy Shaw, H.K. (1966) Notes on Malaysian and Other Asiatic. Euphorbiaceae. *Kew Bulletin* 20: 379–415.
<https://doi.org/10.2307/4108231>
- Airy Shaw, H.K. (1969) New noteworthy species of *Phyllanthus*. *Kew Bulletin* 23: 26–40.
<https://doi.org/10.2307/4108972>
- Airy Shaw, H.K. (1971) Notes on Malesian and Other Asiatic Euphorbiaceae. *Kew Bulletin* 25: 473–553.
<https://doi.org/10.2307/4103199>
- Airy Shaw, H.K. (1972) The Euphorbiaceae of Siam. *Kew Bulletin* 26: 191–363.
<https://doi.org/10.2307/4117717>
- Airy Shaw, H.K. (1974) Notes on Malesian and other Asiatic Euphorbiaceae. *Kew Bulletin* 29: 281–331.
<https://doi.org/10.2307/4108542>
- Airy Shaw, H.K. (1975) The Euphorbiaceae of Borneo. *Kew Bulletin, Additional Series* 4: 1–224.
- Airy Shaw, H.K. (1976) New or noteworthy Australian Euphorbiaceae. *Kew Bulletin* 31: 341–398.
<https://doi.org/10.2307/4109179>
- Airy Shaw, H.K. (1978) Notes on Malesian and other Asiatic Euphorbiaceae. *Kew Bulletin* 33: 361–418.
<https://doi.org/10.2307/4117108>
- Airy Shaw, H.K. (1980a) The Euphorbiaceae of New Guinea. *Kew Bulletin, Additional Series* 8: 3–230.
<https://doi.org/10.2307/4109838>
- Airy Shaw, H.K. (1980b) New Euphorbiaceae from New Guinea. *Kew Bulletin* 34: 591–598.
<https://doi.org/10.2307/4109838>
- Airy Shaw, H.K. (1980c) Notes on Euphorbiaceae from Indomalaysia, Australia and the Pacific. *Kew Bulletin* 35: 383–399.
<https://doi.org/10.2307/4114588>
- Airy Shaw, H.K. (1981) The Euphorbiaceae of Sumatra. *Kew Bulletin* 36: 239–374.
<https://doi.org/10.2307/4113612>
- Airy Shaw, H.K. (1982) The Euphorbiaceae of Central Malesia (Celebes, Moluccas. Lesser Sunda Is.). *Kew Bulletin* 37: 1–40.
<https://doi.org/10.2307/4114718>
- Alston, A.H.G. (1931) Euphorbiaceae. In: Trimen, H. (ed.) *A hand-book to the Flora of Ceylon* 6 (Supplementary). Dulau, London, pp. 255–267.
- André, E.-F. (1883) *Phyllanthus chantrieri*. *Revue Horticole (Paris)* 1883: 537–538, fig. 106, 107.
- Archavaleta y Balpardo, J. (1925) Nueva contribución al conocimiento de la flora del Uruguay. *Anales del Museo de Historia Natural de Montevideo* 1: 72.
- Aublet, J.B.C.F. (1775) *Histoire des Plantes de la Guiane Française* 2. P.F. Didot, Paris, pp. 622–967.
- Baillon, H.E. (1858) *Étude générale du groupe des Euphorbiacées*. Librairie de Victor Masson, Paris, 684 pp.
<https://doi.org/10.5962/bhl.title.50439>
- Baillon, H.E. (1860) Monographie des *Phyllanthus*. *Adansonia* 1: 23–43.
- Baillon, H.E. (1861) Euphorbiaceae Africaines. *Adansonia* 2: 27–55.
- Baillon, H.E. (1862a) Une nouvelle espèce du genre *Menarda*. *Adansonia* 2: 62–64.
- Baillon, H.E. (1862b) Euphorbiaceae Neo-Caledonicae. *Adansonia* 2: 211–242.
- Baillon, H.E. (1865–1866) Euphorbiacées Australiennes. *Adansonia* 6: 282–344.
- Baillon, H.E. (1876) *Stirpes Exoticae novae*. *Adansonia* 11: 365–373.
- Balakrishnan, N.P. & Chakrabarty, T. (2007) *The family Euphorbiaceae in India: A synopsis of its profile, taxonomy and bibliography*. Bishen Singh Mahendra Pal Singh, Dehra Dun, 500 pp.
- Balakrishnan, N.P. & Nair, N.G. (1982) New taxa and record from Saddle Peak, Andaman Islands. *Bulletin of the Botanical Survey of India* 24 (1–4): 28–36.

- Barker, C. & van Welzen, P.C. (2010) *Flueggea* (Euphorbiaceae s.l. or Phyllanthaceae) in Malesia. *Systematic Botany* 35: 541–551.
<https://doi.org/10.1600/036364410792495890>
- Barrett, R.L. & Telford, I.R.H. (2015) Two new species of *Phyllanthus* from northern Australia and notes on *Phyllanthus*, *Sauropus* and *Synostemon* (Phyllanthaceae) in Western Australia. *Nuytsia* 26: 149–166.
- Beille, L. (1908) Euphorbiaceae. In: Chevalier, A. (Ed.) *Novitates florae africanae. Mémoires Société Botanique de France* 8b: 54–85.
<https://doi.org/10.1080/00378941.1907.10833386>
- Beille, L. (1925) Sur quelques Euphorbiacées nouvelles de la flore indo-chinoise. *Bulletin de la Société Botanique de France* 72: 156–163.
<https://doi.org/10.1080/00378941.1925.10832729>
- Beille, L. (1927) *Phyllanthus*. In: Lecomte, M.H. (ed.) *Flore Générale de l'Indo-Chine* 5. Masson, Paris, pp. 571–608.
- Bentham, G. (1842) *Plantas Hartwegianas imprimis Mexicanas*. G. Pamplin, London, 361 pp.
- Bentham, G. (1861) *Flora Hongkongensis: a description of the flowering plants and ferns of the island of Hongkong*. L. Reeve, London, 56 pp.
<https://doi.org/10.5962/bhl.title.55821>
- Bentham, G. (1873) Euphorbiaceae. In: Bentham, G., *Flora Australiensis: a description of the plants of the Australian territory* 6. L. Reeve & Co., London, pp. 41–152.
<https://doi.org/10.1017/CBO9781139096065.005>
- Blanco, F.M. (1837) *Flora de Filipinas*. D. Miquel Sanchez, Manilla, 887 pp.
- Blume, C.L. (1826) *Bijdragen tot de flora van Nederlandsch Indië* 12. Lands Drukkerij, Batavia, pp. 578–636.
<https://doi.org/10.5962/bhl.title.115427>
- Boerlage, J.G. (1900) *Handleiding tot de kennis der flora van Nederlandsch Indië* 3. Voorhees, E.J.Brill, Leiden, 418 pp.
- Bojer, W. (1837) *Hortus Mauritianus*. Imprimerie d'Aimee Mamarot et Compagnie, Maurice, 455 pp.
- Bouman, R., van Welzen, P.C., Sumail, S., Echevarria, G., Erskine, P.D. & van der Ent, A. (2018a) *Phyllanthus rufuschaneyi*: a new nickel hyperaccumulator from Sabah (Borneo Island) with potential for tropical agromining. *Botanical Studies* 59: 9.
<https://doi.org/10.1186/s40529-018-0225-y>
- Bouman, R.W., Keßler, P.J.A., Telford, I.R.H., Bruhl, J.J. & van Welzen, P.C. (2018b). Subgeneric delimitation of the plant genus *Phyllanthus* (Phyllanthaceae). *Blumea* 63: 167–198.
<https://doi.org/10.3767/blumea.2018.63.02.14>
- Bouman, R.W., Keßler, P.J.A., Telford, I.R.H., Bruhl, J.J., Strijk, J.S., Saunders, R.M.K. & van Welzen, P.C. (2021) Molecular phylogenetics of *Phyllanthus* sensu lato (Phyllanthaceae): Towards coherent monophyletic taxa. *Taxon*: 70: 72–98.
<https://doi.org/10.1002/tax.12424>
- Brade, A.C. (1957) Espécies novas da Flora do Brasil. *Archivos do Jardim Botânico do Rio de Janeiro* 15: 5–20.
- Brandegeee, T.S. (1899) New species of plants from Mexico. *Erythraea* 7: 1–8.
- Brandegeee, T.S. (1905) Plants from Sinaloa. *Zoë* 5 (10B): 196–226.
- Brandegeee, T.S. (1914) *Plantae Mexicanae Purpusianae*, VI. *University of California Publications in Botany* 6 (4): 51–77.
- Brandegeee, T.S. (1915) *Plantae Mexicanae Purpusianae* VII. *University of California Publications in Botany* 6 (8): 177–197.
- Brenan, J.P.M. (1950) Plants of the Cambridge Expedition. *Kew Bulletin* 5: 211–226.
<https://doi.org/10.2307/4117228>
- Brenan, J.P.M. (1953) Tropical African Plants: XXIII. *Kew Bulletin* 8: 83–120.
<https://doi.org/10.2307/4117163>
- Brenan, J.P.M. (1954) Plants collected by the Vernay Nyasaland expedition of 1946. *Memoirs of The New York Botanical Garden* 9: 1–484.
- Brenan, J.P.M. (1967) Tropical African Plants XXVIII Euphorbiaceae. *Kew Bulletin* 21: 258–261.
<https://doi.org/10.2307/4108421>
- Britton, N.L. (1920) Descriptions of Cuban plants new to science. *Memoirs of the Torrey Botanical Club* 16: 55–118.
<https://doi.org/10.5962/bhl.title.97213>
- Brown, F.B.H. (1935) Flora of southeastern Polynesia III. Dicotyledons. *Bernice P. Bishop Museum Bulletin* 130: 1–386.
- Brown, N.E., Hutchinson, J. & Prain, D. (1912–1913) Euphorbiaceae. In: Thiselton-Dyer WT (Ed.) *Flora of Tropical Africa* 6 sect. 1 part IV. L. Reeve & Co., London, pp. 441–1094.
- Brown, R. (1810) *Prodromus florae Novae Hollandiae*. J.Johnson & Co., London, pp. 145–590.
- Brown, R. (1849) *Botanical Appendix to Captain Sturt's expedition into central Australia*. G. Norman, London.
- Brunel, J.F. (1980) Notes sur les Phyllanthoideae (Euphorbiaceae) ouest-africaines. IV. *Phyllanthus rouxii* sp. nov., un *Phyllanthus* hémicryptophyte à pivot radicaire tubérisé. *Bulletin de la Société Botanique de France. Lettres Botaniques* 127 (5): 483–491.
<https://doi.org/10.1080/01811797.1980.10824478>

- Brunel, J.F. (1987) *Sur le genre Phyllanthus L. et quelques genres voisins de la tribu des Phyllantheae Dumort. (Euphorbiaceae, Phyllantheae) en Afrique intertropicale et à Madagascar*. Institut de Botanique, Strasbourg, 667 pp.
- Brunel, J.F. & Roux, J. (1977) Notes sur les Phyllanthoideae (Euphorbiaceae) ouest-africaines III. A propos de la position systématique du *Phyllanthus dinklagei* Pax. *Bulletin de la Société Botanique de France* 124: 217–225.
<https://doi.org/10.1080/00378941.1977.10835744>
- Brunel, J.F. & Roux, J. (1981) *Phyllanthus* subsect. *Odontadenii* (Euphorbiaceae) au nord du fleuve Congo (Afrique de l'Ouest). *Willdenowia* 11: 69–90.
- Brunel, J.F. & Roux, J. (1984) South-east Asian Phyllantheae. II. Some *Phyllanthus* of subsect. *Swartziani*. *Nordic Journal of Botany* 4: 469–473.
<https://doi.org/10.1111/j.1756-1051.1984.tb02049.x>
- Brunel, J.F. & Roux, J. (1985) Les *Phyllanthus* (Euphorbiaceae) affines de la section *Anisolobum* en Afrique intertropicale. Beiträge zur Flora von West-Afrika 18. *Willdenowia* 15: 235–254.
- Buchanan-Hamilton, F. (1825) *Prodromus Florae Nepalensis*. J.Gale, London, 256 pp.
- Buchanan-Hamilton, F. (1827) A commentary on the Third Part of the Hortus Malabaricus. *Transactions of the Linnean Society of London* 15: 78–152.
<https://doi.org/10.1111/j.1095-8339.1826.tb00110.x>
- Casaretto, G. (1845) *Novarum Stirpium Brasiliensium Decades*. Typis Joannis Ferrandi, Genuae, 96 pp.
- Chakrabarty, T. & Balakrishnan, N.P. (2009) Transfer of Indian species of *Breynia*, *Glochidion* and *Sauropus* to *Phyllanthus* (Phyllanthaceae)- new combinations and new names. *Journal of Economic and Taxonomic Botany* 33: 712–716.
- Chakrabarty, T. & Balakrishnan, N.P. (2012) Nineteen new combinations and a new name in *Breynia* J.R. Forst. & G. Forst. (Phyllanthaceae) from Indian subcontinent. *Bangladesh Journal of Plant Taxonomy* 19: 119–122.
<https://doi.org/10.3329/bjpt.v19i2.13125>
- Chakrabarty, T. & Balakrishnan, N.P. (2018) *Indo-Burmese Phyllanthaceae*. Bishen Singh Mahendra Pal Singh, Dehra Dun, 431 pp.
- Chakrabarty, T. & Gangopadhyay, M. (1993) A new *Phyllanthus* L. (Euphorbiaceae) from North Andaman island. *The Journal of the Bombay Natural History Society* 90: 69–70.
- Challen, G., Vorontsova, M.S., Schneider, H. & Cheek, M. (2011) Phylogenetically distinct and critically endangered new tree species of *Phyllanthus* from Cameroon (Phyllanthaceae, Euphorbiaceae s.l.). *Systematic Botany* 36: 933–938.
<https://doi.org/10.1600/036364411X604949>
- Chantaranothai, P. (2007) *Phyllanthus*. In: van Welzen, P.C. & Chayamarit, K. (eds.) Euphorbiaceae. In: Santisuk, T., Larsen, K. (Eds.) *Flora of Thailand* 8 (2). The Forest Herbarium, Bangkok, pp. 473–507.
- Chaudhary, L.B. & Rao, R.R. (2002) Taxonomic study of herbaceous species of *Phyllanthus* L. (Euphorbiaceae) in India. *Phytotaxonomy* 2: 143–162.
- Chiovenda, E. (1929) *Flora Somalia* 1. Sindacata Italiano Arti Grafiche, Roma, 436 pp.
- Chodat, R. & Hassler, E. (1905) Plantae Hasslerianae soit Énumération des plantes récoltées au Paraguay. *Bulletin de l'Herbier Boissier sér. 2*, 5: 288–506.
- Colla, L. (1836) *Herbarium Pedemontanum* 5. Ex Typis Regis, Torino, 563 pp.
- Collet, H. & Hemsley, W.B. (1890) On a collection of plants from Upper Burma and the Shan States. *Journal of the Linnean Society, Botany* 28: 1–150.
<https://doi.org/10.1111/j.1095-8339.1890.tb01452.x>
- Coode, M.J. (1978) Notes on Euphorbiaceae in the Mascarene Islands: I. *Kew Bulletin* 33: 109–120.
<https://doi.org/10.2307/4110107>
- Cordeiro, I. & Carneiro-Torres, D.S. (2004) A new species of *Phyllanthus* (Phyllanthaceae) from Chapada Diamantina, Bahia, Brazil. *Botanical Journal of the Linnean Society* 146: 247–250.
<https://doi.org/10.1111/j.1095-8339.2004.00316.x>
- Craib, W.G. (1911) In: A.F.G. Kerr: Contributions to the Flora of Siam. *Bulletin of Miscellaneous Information, Kew* 1911: 385–473.
<https://doi.org/10.2307/4115077>
- Craib, W.G. (1913) Contributions to the Flora of Siam: VI. *Bulletin of Miscellaneous Information, Kew* 1913: 65–72.
<https://doi.org/10.2307/4111652>
- Craib, W.G. (1914) Contributions to the Flora of Siam: VII. *Bulletin of Miscellaneous information, Kew* 1914: 279–285.
<https://doi.org/10.2307/4118550>
- Craib, W.G. & Hutchinson, J. (1910) Decades Kewenses: LV. *Bulletin of Miscellaneous Information, Kew* 1910: 19–23.
<https://doi.org/10.2307/4115018>
- Croizat, L.C.M. (1942a) On certain Euphorbiaceae from the tropical Far East. *Journal of the Arnold Arboretum* 23: 29–54.
<https://doi.org/10.5962/p.185450>

- Croizat, L.C.M. (1942b) *Euphorbiaceae*. In: Smith, A.C. Fijian plant studies II. *Sargentia* 1: 46–52.
- Croizat, L.C.M. (1943a) Notes on Polynesian *Glochidion* and *Phyllanthus*. *Occasional papers of the Bernice Pauahi Bishop Museum of Polynesian Ethology and Natural History* 17: 207–214.
- Croizat, L.C.M. (1943b) Notes on American Euphorbiaceae, with descriptions of eleven new species. *Journal of the Washington Academy of Sciences* 33: 11–20.
- Croizat, L.C.M. (1944) Three new Amazonian species of *Phyllanthus* L. *Tropical Woods* 78: 5–9.
- Croizat, L.C.M. (1945) New or critical Euphorbiaceae from the Americas. *Journal of the Arnold Arboretum* 26: 181–196.
<https://doi.org/10.5962/bhl.part.13121>
- Croizat, L.C.M. (1946) Especies nuevas de la Comision Botanica del Valle del Cauca. (Colombia). *Ciencia (Mexico)* 6: 353–354.
- Croizat, L.C.M. & Metcalf, F.P. (1942) Novelties in Chinese *Phyllanthus*. *Lingnan Science Journal* 20: 193–198
- Cufodontis, G. (1947) Die botanischen Ergebnisse von Fr. J. Bieber's Reisen in Äthopien. *Sitzungsberichte. Akademie der Wissenschaften in Wien. Mathematisch-naturwissenschaftliche Klasse. Abteilung I. Biologie* 156: 461–498.
- Däniker, A.U. (1931) Ergebnisse der Reise von Dr. A. U. Däniker nach Neu-Kaledonien und den Loyalitäts-Inseln (1924/25). 2. Neue Phanerogamen von Neu-Kaledonien und den Loyalitäts-Inseln. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* 76: 160–170.
- Das, A. (1940) Euphorbiaceae. In: Kunjilal, U.N. et al. (Eds.) *Flora of Assam 4: Nyctaginaceae to Cycadaceae*. R.C. Roy Choudhury Prabashi Press, Calcutta, pp. 135–233.
- De Wildeman, E.A.J. (1906) *Études de systematique et de géographie botaniques sur la flore de Bas- et du Moyen-Congo I*. Par ordre du Secreitaire d'Eitats, Bruxelles, 344 pp.
- Desvaux, N.A. (1818) *Observations sur les plantes des environs d'Angers*. Fourier-Mame, Angers & Dondey-Dipré, Paris, 188 pp.
- Diels, F.L.E. (1931) Aufklärung der Gattung *Leichhardtia* F.v.M. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 11: 308–310.
<https://doi.org/10.2307/3994750>
- Dinter, K. (1926) Index der aus Deutsch-Südwestafrika bis zum Jahre 1917 bekannt gewordenen Pflanzenarten. XIX. *Repertorium specierum novarum regni vegetabilis* 22: 375–383.
<https://doi.org/10.1002/fedr.19260222214>
- Domin, K. (1927) Beiträge zur Flora und Planzengeographie Australiens. *Bibliotheca Botanica* 89: 91
- Don, D. (1825) *Prodromus Florae Nepalensis*. J.Gale, Londen, 256 pp.
- Dujardin, F. (1841) *Histoire Naturelle des Zoophytes*. Librairie Encyclopédique de Roret, Paris, xii + 684 pp.; *Atlas*: 22 pls.
- Elmer, A.D.E. (1908) A Century of new plants. *Leaflets of Philippines Botany* 1: 272–360.
- Elmer, A.D.E. (1910) Euphorbiaceae collected on Sibuyan Island. *Leaflets of Philippine Botany* 3: 901–931.
- Elmer, A.D.E. (1911) Euphorbiaceae collected on Palawan Island. *Leaflets of Philippine Botany* 4: 1271–1306.
- Falcón, B., Gómez Hechavarría, J.L. & Fuentes Bazan, S. (2017) *Phyllanthus phialanthoides* (Phyllanthaceae), a new species from northeastern Cuba. *Revista del Jardín Botánico Nacional* 38: 1-6.
- Falcón, B. & Leyva, L.M. (2020) Nuevos datos acerca de *Phyllanthus pseudocicca* (Phyllantaceae). *Revista Jardín Botánico Nacional* 41: 141–146.
- Falcón, B., Fuentes, S.B., Berazaín, R.I. & Borsch, T. (2020) Phylogenetic relationships and character evolution in Neotropical *Phyllanthus* (Phyllanthaceae), with a focus on the Cuban and Caribbean taxa. *International Journal of Plant Sciences* 181 (3): 384–305.
<https://doi.org/10.1086/706454>
- Farr, E.R. & Zijlstra, G. (eds.) (1996+) *Index Nominum Genericorum (Plantarum)*. Natural Museum of National History, Smithsonian Institution, Washington D.C. Available at <http://botany.si.edu/ing/> (accessed March 2019).
- Florence, J. (1996) Gallicae Polynesiæ floræ Præcursores. Novevautés taxonomiques dans les Euphorbiaceae, Piperaceae et Urticaceae. *Bulletin du Muséum National d'Histoire Naturelle, Section B, Adansonia. sér. 4, Botanique Phytochimie* 18: 239–274.
- Florence, J. (1997a) Euphorbiaceae. In: Florence, J. (Ed.) *Flore de la Polynésie Française*. Orstrom éditions, Paris, pp. 27–141.
- Florence, J. (1997b). New species of *Alyxia* Banks ex R. Brown (Apocynaceae) and *Glochidion* J.R. & J.G.Forster (Euphorbiaceae) from the Pitcairn Islands (South East Pacific). *Novon* 7: 27–31.
<https://doi.org/10.2307/3392069>
- Forsskål, P. (1775) *Flora aegyptiaco-arabica*. (ed. by C. Niebuhr). Möller, Kjobenhavn, 219 pp.
- Forster, G. (1786) *Florulae insularum Australium Prodromus*. J. C, Dieterich, Goettingen, 103 pp.
<https://doi.org/10.5962/bhl.title.10725>
- Forster, J.R. & Forster, G. (1776) *Characteres Generum Plantarum ed. 2*. J.R. & G. Forster, London, 150 pp.
- Fosberg, F.R. (1978) Miscellaneous notes on the Flora of Aldabra and Neighbouring Islands: XI. Critical notes on Euphorbiaceae. *Kew Bulletin* 33: 181–190.
<https://doi.org/10.2307/4109574>

- Fosberg, F.R. & Oliver, R.L. (1991) C.L. Ledermann's collection of flowering plants from the Caroline Islands. *Willdenowia* 20: 257–314.
- Fries, R.E. (1914) *Wissenschaftliche Ergebnisse der Schwedischen Rhodesia-Kongo-Expedition, 1911–1912, unter Leitung von Eric Graf von Rosen* 1.1. Aftonbladets Druckerei, Stockholm, pp. 1–184.
- Funez, L.A., Ferreira, J.P.R. & Hassemer, G. (2018) *Phyllanthus timboënsis* (Phyllanthaceae), a new species from Santa Catarina, southern Brazil. *Webbia* 73: 63–69.
<https://doi.org/10.1080/00837792.2018.1452370>
- Funez, L.A. & Hassemer, G. (2017) *Phyllanthus eremitus* (Phyllanthaceae), a narrowly endemic new species from Santa Catarina, southern Brazil, and lectotypification and range extension of *P. hyssopifolioides*. *Phytotaxa* 319: 149–158.
<https://doi.org/10.11646/phytotaxa.319.2.3>
- Gaertner, J. (1790) *De fructibus et seminibus plantarum* 2(1). G.H. Schramm, Tübingen, pp. 1–184, pl. 80–119.
- Gage, A.T. (1914) New Euphorbiaceae from India and Malaya. *Bulletin of Miscellaneous Information, Kew* 1914: 236–241.
<https://doi.org/10.2307/4119465>
- Gage, A.T. (1917) Euphorbiaceae. Nova Guinea 12: 479–486.
- Gagnepain, F. (1950) Genres nouveaux, Espèces nouvelles d'Indochine (Ile P.). *Notulae Systematicae (Paris)* 14: 22–37.
- Gamble, J.S. (1925) *Flora of the Presidency of Madras*. Adlard & Son, London, 577 pp.
- Gibbs, L.Z. (1909) A contribution to the Montane Flora of Fiji (including Cryptogams) with Ecological Notes. *Journal of the Linnean Society, Botany* 39: 130–212.
<https://doi.org/10.1111/j.1095-8339.1909.tb01192.x>
- Gilbert, M.G. (1987) New and interesting species of Euphorbiaceae from Ethiopia. *Kew Bulletin* 42: 351–368.
<https://doi.org/10.2307/4109690>
- Gilbert, M.G. & Li, P.T. (2008) *Phyllanthus rheophyticus*. In: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (Eds.) *Flora of China* 11. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis, p. 188.
- Gilbert, M.G. & Thulin, M. (1993) A new species of *Phyllanthus* (Euphorbiaceae) from Somalia. *Nordic Journal of Botany* 13: 171–173.
<https://doi.org/10.1111/j.1756-1051.1993.tb00032.x>
- Gillespie, J.W. (1932) New plants from Fiji—III. *Bernice P. Bishop Museum Bulletin* 91: 1–81.
- Glassman, S.F. (1952) The flora of Ponape. *Bernice P. Bishop Museum Bulletin* 209: 1–152.
- Gleason, H. (1931) Botanical results of the Tyler-Duida Expedition (Continued). *Bulletin of the Torrey Botanical Club* 58: 345–404.
<https://doi.org/10.2307/2480734>
- Gmelin, J.F. (1791) *Caroli à Linné Systema Naturae* 2. Georg. Emanuel. Beer, Leipzig, 884 pp.
- Govaerts, R.H.A. (2018) 101 Nomenclatural Corrections in Preparation for the Plants of the World Online (POWO). *Skortsovia* 4: 74–99.
- Govaerts, R.H.A. & Radcliffe-Smith, A. (1996) New names and combinations in Euphorbiaceae—Phyllanthoideae. *Kew Bulletin* 51: 175–178.
<https://doi.org/10.2307/4118755>
- Graham, J. (1839) *A Catalogue of the plants growing in Bombay and its vicinity*. Government Press, Bombay, 521 pp.
- Grande, J.R., Kallunki, J., Arbo, M.M., Berry, P.E., Huber, O. & Riina, R. (2012) Botanical novelties from Sierra de Maigualida, southern Venezuela. II. *Anales del Jardín Botánico de Madrid* 69: 7–19.
<https://doi.org/10.3989/ajbm.2299>
- Grandidier, A. (1892), *Histoire physique, naturelle et politique de Madagascar. Histoire des plantes* 34 (2), *Atlas* 2: pl. 295–241.
- Gray, A. (1880) Contributions to North American botany. *Proceedings of the American Academy of Arts and Sciences* 16: 78–108.
<https://doi.org/10.2307/25138603>
- Greenman, J.M. (1898) Diagnoses of new and critical Mexican Phanerogams. *Proceedings of the American Academy of Arts and Sciences* 33 (25): 453–490.
<https://doi.org/10.2307/20020832>
- Griffith, W. (1848) Itinerary Notes of Plants Collected in the Khasyah and Bootan Mountains. Posthumous Papers bequeathed to the honourable, the East India Company, vol. 2. J.F. Bellamy, Calcutta, 435 pp.
- Griffith, W. (1854) *Notulae ad plantas asiaticas* 4. Bishop's college Press, Calcutta, 764 pp.
- Grisebach, A.H.R. (1859) *Flora of the British West Indian Islands* 1. Lovell Reeve & Co., London, pp. 1–96.
- Grisebach, A.H.R. (1860) *Plantae Wrightianae* 1. Cambridge, Boston (= *Memoirs of the American Academy of Arts and Sciences, ser. 2*, 8: 153–192)
- Grisebach, A.H.R. (1865) Diagnosen neuer Euphorbiaceen aus Cuba. *Nachrichten von der Königlich-Gesellschaft der Wissenschaften und der Georg-August-Universität zu Göttingen* 1: 161–181.
- Guillaumin, A. (1913) Species Montrouzieranae. *Annales de la Société Botanique de Lyon* 38: 75–125.

<https://doi.org/10.3406/linly.1914.15624>

- Guillaumin, A. (1927) Contribution a la Flore de la Nouvelle Calédonie. *Bulletin du Muséum National d'Histoire Naturelle* 33: 272–276.
- Guillaumin, A. (1929) Revision de Euphorbiacées de la Nouvelle-Caledonie. *Archives de Botanique, Mémoires* 2 (3): 1–48.
- Guillaumin, A. (1962) Resultats scientifiques de la mission Franco-suisse de botanique en Nouvelle-Caledonie. *Mémoires du Muséum National d'Histoire Naturelle. Nouvelle Série. Série B, Botanique* 8, no. 3: 193–392.
- Handel-Mazzetti, H.R.E. von (1931) *Symbolae Sinicae* 7 (2). Julius Springer, Wien, pp. 211–448.
- Hara, H. (1966) *The flora of the Eastern Himalaya*. University of Tokyo Press, Tokyo, 746 pp.
- Hasskarl, J.C. (1843) Annotationes de plantis quibusdam Javanicis nonnullisque Japonicis, e Catalogo Horti Bogoriensis. Accedunt nonnullae novae species. *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie* 10: 115–150.
- Hasskarl, J.C. (1844) *Catalogus Plantarum in Horto Botanico Cultarum Alter*. Lands Drukkerij, Batavia, 391 pp.
<https://doi.org/10.5962/bhl.title.79159>
- Hayata, B. (1904) Revisio Euphorbiacearum et Buxacearum Japonicarum. *Journal of the College of Science, Imperial University of Tokyo* 20 (3): 1–92.
- Hayata, B. (1920) *Icones Plantarum Formosanarum* 9. Government of Formosa, Taihoku, pp. 1–155.
- Hemsley, W.B. (1898) *Phyllanthodendron mirabilis* Hemsl. *Hooker's Icones Plantarum* 26: tab. 2563–2564.
- Henry, A.N., Kumari, G.R. & Chithra, V. (1987) *Flora of Tamil Nadu, India, ser. 1, 2*. Botanical Survey of India, Coimbatore.
- Henry, A.N., Vivekananthan, K. & Nair, N.C. (1979) Rare and threatened flowering plants of South India. *The Journal of the Bombay Natural History Society* 75: 684–698.
- Hermann, P. (1717) *Musaeum Zeylanicum*. Severinus, Lugduni Batavorum [Leiden], 71 pp.
- Hoffmann, P. (2008) Revision of *Heterosavia*, stat. nov., with notes on *Gonatogyne* and *Savia* (Phyllanthaceae). *Brittonia* 60: 136–166.
<https://doi.org/10.1007/s12228-008-9012-5>
- Hoffmann, P. & Cheek, M. (2003) Two new species of *Phyllanthus* (Euphorbiaceae) from southwest Cameroon. *Kew Bulletin* 58: 437–446.
<https://doi.org/10.2307/4120626>
- Hoffmann, P., Kathirarachchi, H. & Wurdack, K.J. (2006) A phylogenetic classification of Phyllanthaceae (Malpighiales; Euphorbiaceae sensu lato). *Kew Bulletin* 61: 37–53.
- Hoffmann, P., Baker, A.J., Madulid, D.A. & Proctor, J. (2003) *Phyllanthus balgooyi* (Euphorbiaceae s.l.), a new nickel-hyperaccumulating species from Palawan and Sabah. *Blumea* 48 (1): 193–199.
<https://doi.org/10.3767/000651903X686178>
- Holm-Nielsen, L.B. (1979) Comments on the distribution and evolution of the genus *Phyllanthus* (Euphorbiaceae). In: Larsen, K. & Holm-Nielsen, L.B. (Eds.) *Tropical Botany*. Academic Press, New York, pp. 277–290.
- Hooker, J.D. (1846) An enumeration of the plants of the Galapagos Archipelago; with descriptions of those which are new. *Transactions of the Linnean Society of London* 20: 163–234.
<https://doi.org/10.1111/j.1096-3642.1846.tb00416.x>
- Hooker, J.D. (1847) Florae Tasmaniae Spicilegium; or contributions towards a Flora of Van Diemen's Land. *London Journal of Botany* 6: 265–286.
- Hooker, J.D. (1887) Euphorbiaceae. In: Hooker, J.D., *The Flora of British India* 5. L. Reeve & Co, London, pp. 241–462.
- Hooker, W.J. & Walker-Arnott, G.A. (1832) *The Botany of Captain Beechey's voyage* 2. Henry G. Bohn, London, pp. 49–96, pl. 11–20.
- Hornemann, J.W. (1807) *Enumeratio Plantarum Horti Botanici Hafniensis, rev. ed.* J.F. Schultz, Kjøbenhavn [Copenhagen] 79 pp.
- Hosokawa, T. (1935) Materials of the botanical research towards flora of Micronesia III. *Transactions, Natural History Society of Formosa* 25: 17–39.
- Howard, R.A. (1947) Notes on some plants of Cuba. *Journal of the Arnold Arboretum* 28: 117–126.
<https://doi.org/10.5962/p.185568>
- Hunter, J.T. & Bruhl, J.J. (1996) Three new species of *Phyllanthus* (Euphorbiaceae: Phyllanthaceae) in South Australia. *Journal of the Adelaide Botanic Garden* 17: 127–136.
- Hunter, J.T. & Bruhl, J.J. (1997a). Four new rare species of *Sauropus* Blume (Euphorbiaceae: Phyllanthaceae) from north Queensland. *Austrobaileya* 4: 661–672.
- Hunter, J.T. & Bruhl, J.J. (1997b) Three new species of *Phyllanthus* (Euphorbiaceae: Phyllanthaceae) for the Northern Territory, one new species for Western Australia, and notes on other *Phyllanthus* species occurring in these regions. *Nuytsia* 11: 147–163.
- Hunter, J.T. & Bruhl, J.J. (1997c) Two new species of *Phyllanthus* and notes on *Phyllanthus* and *Sauropus* (Euphorbiaceae: Phyllanthaceae) in New South Wales. *Telopea* 7: 149–165.
<https://doi.org/10.7751/telopea19971006>
- Hutchinson, J. (1911) Diagnoses Africanæ XLIV. *Bulletin of Miscellaneous Information, Kew* 1911: 313–318.
<https://doi.org/10.2307/4119482>

- Hutchinson, J. (1913) Euphorbiaceae. In: Oliver, D. *Flora of Tropical Africa* 6 (1). Lovell Reeve & Co., London, pp. 769–960.
- Hutchinson, J. (1920) Diagnoses Africanæ: LXXIII. *Bulletin of Miscellaneous Information, Kew* 1920: 23–28.
<https://doi.org/10.2307/4119514>
- Hutchinson, J. & Dalziel, J.M. (1928) *Flora of West Tropical Africa* 1 (2). The Crown Agents for the Colonies, London, pp. 247–523.
- Hutchinson, J. & De Wildeman, E.A.J. (1932) In: De Wildeman, E.A.J., *Plantae Bequaertianae* 5 (4). Royal Museum for Central Africa, Tervuarem, pp. 1–91.
- Jablonski, E. (1967) Euphorbiaceae. In: Maguire, B. *et al.* (eds.) The botany of the Guayana Highland—part VII. *Memoirs of the New York Botanical Garden* 17: 80–190.
- Jablonski, E. (1972) Euphorbiaceae. In: Steyermark, J.A. & Maguire, B. (Eds.) The flora of the Meseta del Cerro Jaua. *Memoirs of The New York Botanical Garden* 23: 864–866.
- Jacquín, N.J. von (1797) *Plantarum Rariorum Horti Caesarei Schoenbrunnensis descriptiones et icones* 2. Apud C.F. Wappler, Viennæ, 68 pp.
<https://doi.org/10.5962/bhl.title.332>
- Johnston, M.C. (1985) *Phyllanthus fraguensis* (Euphorbiaceae), a new species from the Chihuahuan Desert Region. *Systematic Botany* 10: 300–302.
<https://doi.org/10.2307/2418593>
- Johnston, M.C. (1986) *Phyllanthus barbarae* (Euphorbiaceae), new species from Southwestern Tamaulipas, Mexico. *Systematic Botany* 11: 35–38.
<https://doi.org/10.2307/2418943>
- Jussieu, A.L. de (1789) *Genera plantarum secundum ordines naturales disposita*. Herissant & Barrois, Paris, 1428 pp.
- Jussieu, A.H.L. de (1823) Considérations sur la Famille des Euphorbiacées. *Mémoires du Muséum d'Histoire Naturelle* 10: 317–355.
- Jussieu, A.H.L. de (1824) *De Euphorbiacearum generibus medicisque earumdem viribus tentamen*. Didot, Paris, 118 pp.
<https://doi.org/10.5962/bhl.title.51511>
- Kantachot, C. & Chantaranothai, P. (2013) A new species of *Phyllanthus chayamaritiae* (Phyllanthaceae) from Thailand. *Blumea* 57: 217–220.
<https://doi.org/10.3767/000651913X663280>
- Kato, M. & Kawakita, A. (2017) *Obligate pollination mutualism*. Springer, Tokyo, 310 pp.
<https://doi.org/10.1007/978-4-431-56532-1>
- Kato, M., Takumura, A. & Kawakita, A. (2003) An obligate pollination mutualism and reciprocal diversification in the tree genus *Glochidion* (Euphorbiaceae). *Proceedings of the National Academy of Sciences, USA* 100: 5264–5267.
<https://doi.org/10.1073/pnas.0837153100>
- Kawakita, A. & Kato, M. (2009) Repeated independent evolution of obligate pollination mutualism in the Phyllanthaceae—Epiccephala association. *Proceedings of the Royal Society B: Biological Sciences* 276: 417–426.
<https://doi.org/10.1098/rspb.2008.1226>
- Klotzsch, J.F. (1841) Neue und weniger gekannte südamerikanische Euphorbiaceen-Gattungen. *Archiv für Naturgeschichte* 7: 175–247.
- Klotzsch, J.F. (1843) Euphorbiaceae. In: Bentham, G. *et al.* (Ed.)s, Contributions towards a Flora of South America—Enumeration of plants collected by Mr. Schomburgk, in British Guiana. *London Journal of Botany* 2: 42–52.
- Klotzsch, J.F. (1845) Euphorbiaceae. In: Lehmann, J.G.C. *Plantae preissianae* 1 (2). Sumptibus Meissneri, Hamburgi pp. 175–180.
- Koorders, H.S. (1898) Verslag eener botanische dienstreis door de Minahassa. *Mededeelingen Lands Plantentuin* 19: 1–716.
- Kunth, K.S. (1817) Euphorbiaceae. In: Humboldt, F.W.H.A. von, Bonpland, A.J.A. & Kunth, K.S. (Eds.) *Nova Genera et Species Plantarum* (quarto ed.) 2. Librairie Grecque-Latine Allemande, Paris, pp. 51–118.
- Kuntze, O. (1891) *Revisio generum plantarum* 2. A. Felix, Leipzig, pp. 377–1011.
- Kurosawa, T. (2016) Transfer of Japanese *Breynia* and *Glochidion* to *Phyllanthus* (Phyllanthaceae). *Journal of Japanese Botany* 91: 118–121.
- Kurz, W.S. (1870) *Report on the Vegetation of the Andaman Islands*. Office of Superintendent of Government Printing, Calcutta, 75 pp.
- Kurz, W.S. (1873) New Burmese plants, part III. *Journal of the Asiatic Society of Bengal, Part 2, Natural History* 42: 227–254.
- Kurz, W.S. (1877) *Forest Flora of British Burma* 2. Government printing, Calcutta, 613 pp.
<https://doi.org/10.5962/bhl.title.52413>
- Labillardière, J.J.H. (1806) *Novae Hollandiae Plantarum Specimen* 2. Ex typographia Dominae Huzard, Paris, 133 pp.
- Lamarck, J.B.A.P.M. (1804) *Encyclopédie méthodique. Botanique* 5. Panckoucke, Paris & Plomteux, Liège, pp. 1–748.
- Lasser, T. & Maguire, B. (1950) A report on the plants of the Phelps Cerro Yavi Expedition of 1947. *Brittonia* 7: 75–90.
<https://doi.org/10.2307/2804931>
- Leandri, J.D. (1933) Nouveaux *Phyllanthus* de Madagascar. *Bulletin de la Société Botanique de France* 80: 371–373.
<https://doi.org/10.1080/00378941.1933.10833852>

- Leandri, J.D. (1934) Espèces et localités nouvelles d'Euphorbiacées d'Afrique et Madagascar. *Bulletin de la Société Botanique de France* 81: 449–454.
<https://doi.org/10.1080/00378941.1934.10833978>
- Leandri, J.D. (1935) *Catalogue des Plantes de Madagascar, Euphorbiaceae*. Imprimerie G. Pitot, Tananarive, 51 pp.
- Leandri, J.D. (1937) Contribution à l'étude des Euphorbiacées de Madagascar. *Notulae Systematicae (Paris)* 6: 11–35.
- Leandri, J.D. (1938) Contribution à l'étude des Euphorbiacées de Madagascar (suite). *Notulae Systematicae (Paris)* 6: 185–199.
- Leandri, J.D. (1957) Notes systematiques sur les Euphorbiacées-Phyllanthées de Madagascar. *Mémoires de l'Institut Scientifique de Madagascar. Série B. Biologie Végétale* 8: 205–261.
- Leandri, J.D. (1958) Euphorbiaceae I (Phyllanthoidea). In: Humbert, H. (Eds.) *Flore de Madagascar et Comores, 111ème famille* 1. Firmin Didot, Paris, pp. 1–199.
- Léveillé, A.A.H. (1911) Decades plantarum novarum LIV–LVIII. *Repertorium Specierum Novarum Regni Vegetabilis* 9: 324–330.
<https://doi.org/10.1002/fedr.19110091909>
- Léveillé, A.A.H. (1915a) *Flore du Kouy-Tchéou*. Le Mano, Paris, 535 pp.
- Léveillé, A.A.H. (1915b) Flora missionaria asiatica. *Bulletin de Géographie Botanique; Organe Mensuel de l'Académie Internationale de Botanique* 25: 20–26.
- L'Heurtelet de Brutelle, C.L. (1778) *Sertum Anglicumi*. F. Didot, Paris, 20 pp.
- Li, P.T. (1982) New names for three species of Euphorbiaceae. *Acta Phytotaxonomica Sinica* 20: 117.
- Li, P.T. (1983) Materials for the Euphorbiaceae of Guangxi. *Guihaia* 3: 167–170.
- Li, P.T. (1987a) A revision of Chinese *Phyllanthus* (Euphorbiaceae). *Acta Phytotaxonomica Sinica* 25: 371–371.
- Li, P.T. (1987b) A revision of the Chinese *Phyllanthodendron* (Euphorbiaceae). *Bulletin of Botanical Research* 7: 1–9.
- Lindberg, S.O. (1868) Musci novi Scandinaviei. *Notiser ur Sällskapetets pro Fauna et Flora Fennica Förhandlingar* 9: 253–300.
- Lindley, J. (1828) An account of a new genus of plants, named *Macraea*. *Quarterly Journal of Science, Literature and the Arts ser. 2*, 1: 104–106.
- Linnaeus, C. (1753) *Species Plantarum*. Laurentius Salvius, Stockholm, 1200 pp.
- Linnaeus, C. (1767) *Systema Naturae* ed. 12, 2. Laurentius Salvius, Stockholm, pp. 533–1327.
- Linnaeus, C. (1771) *Mantissa plantarum altera*. Laurentius Salvius, Stockholm, pp. 143–588.
- Linnaeus fill., C. (1782) *Supplementum plantarum*. Impensis Orphanotropei, Brunsvigae [Braunschweig], 468 pp.
- Lisowski, S., Malaisse, F. & Symoens, J. (1974) Sur la découverte d'un *Phyllanthus* aquatique des Hauts plateaux du Shabha (Zaïre). *Bulletin De La Société Royale De Botanique De Belgique / Bulletin Van De Koninklijke Belgische Botanische Vereniging* 107 (1): 199–202.
- Llanos, A. (1857) Columniferae Sterculiae. *Botanische Zeitung* 15: 423.
- Lobreau-Callen, D., Punt, W. & Schmid, M. (1988) Pollen morphology and taxonomy of the *Phyllanthus* species (Euphorbiaceae) native to New Caledonia. *Review of Palaeobotany and Palynology* 53: 283–304.
[https://doi.org/10.1016/0034-6667\(88\)90036-X](https://doi.org/10.1016/0034-6667(88)90036-X)
- Loureiro, J.F. de (1790) *Flora Cochinchinensis* 1. J. de Loureiro, Lissabon, pp. 1–353.
- Lundell, C.L. (1985) Euphorbiaceae from Mesoamerica. *Phytologia* 57: 367–368.
- Luo, S.-X., Yao, G., Wang, Z., Zhang, D. & Hembry, D.H. (2017) A novel, enigmatic basal leafhopper moth lineage pollinating a derived leafhopper host illustrates the dynamics of host shifts, partner replacement, and apparent coadaptation in intimate mutualisms. *The American Naturalist* 189: 422–435.
<https://doi.org/10.1086/690623>
- Macbride, J.F. (1951) Flora of Peru. *Publications of the Field Museum of Natural History, Botanical Series 13 part 3A* number 1. 288 pp.
- Maddison, W.P. & Maddison, D.R. (2019) Mesquite: a modular system for evolutionary analysis. Version 3.61 <http://www.mesquiteproject.org>
- Malme, G.O.A. (1905) Adnotationes de nonnullis Asclepiadaceis austroamericanis. *Arkiv för Botanik* 4 (14): 1–19.
- Mansfeld, R. (1933) In: Schmidt, O.C., Beiträge zur Kenntnis der Flora Westindiens. VI. *Repertorium Specierum Novarum Regni Vegetabilis* 32: 73–94.
<https://doi.org/10.1002/fedr.19330320103>
- Marques Torres, A.M., Silva, M.J., Cordeiro, W.P.F.D.S., Athie-Souza, S.M. & Sales, M.F. (2020) Two new species of *Phyllanthus* (Phyllanthaceae) endemic to the Brazilian Atlantic Rainforest. *Phytotaxa* 458: 173–181.
<https://doi.org/10.11646/phytotaxa.458.2.5>
- Mathew, J. & Yohannan, R. (2021) *Phyllanthus sanatanadharmae* (Phyllanthaceae): a new species from southern Western Ghats, India. *Phytotaxa* 498 (4): 290–294.
<https://doi.org/10.11646/phytotaxa.498.4.7>

- McPherson, G. & Schmid, M. (1991) *Flore de la Nouvelle Calédonie et Dépendances 17: Euphorbiaceae*. Muséum National d'Histoire Naturelle, Paris, 329 pp.
- McVaugh, R. (1961) Euphorbiaceae Novae Novo-Galicianae. *Brittonia* 13: 145–205.
<https://doi.org/10.2307/2805352>
- Meewis, B. & Punt, W. (1983) Pollen morphology and taxonomy of the subgenus *Kirganelia* (Jussieu) Webster (genus *Phyllanthus*, Euphorbiaceae) from Africa. *Review of Palaeobotany and Palynology* 39: 131–160.
[https://doi.org/10.1016/0034-6667\(83\)90014-3](https://doi.org/10.1016/0034-6667(83)90014-3)
- Merrill, E.D. (1906) The Flora of the Lamao Forest Reserve. *The Philippine Journal of Science* 1, Supplement 1: 1–142.
- Merrill, E.D. (1912) Notes on Philippine Euphorbiaceae. *The Philippine Journal of Science, Section C, Botany* 7: 379–410.
- Merrill, E.D. (1914) An enumeration of the plants of Guam. *The Philippine Journal of Science, Section C, Botany* 9: 97–156.
- Merrill, E.D. (1917) *An interpretation of Rumphius's Herbarium amboinense*. Bureau of Printing, Manilla, 595 pp.
<https://doi.org/10.5962/bhl.title.79163>
- Merrill, E.D. (1920) Notes on Philippine Euphorbiaceae, III. *The Philippine Journal of Science* 16: 539–580.
<https://doi.org/10.5962/bhl.part.4748>
- Merrill, E.D. (1925) Additions to our knowledge of the Philippine flora, I. *The Philippine Journal of Science* 26: 447–496.
- Merrill, E.D. (1926) Additions to our knowledge of the Philippine flora, III. *The Philippine Journal of Science* 30: 389–430.
- Merrill, E.D. (1935) A sixth supplementary list of Hainan Plants. *Lingnan Science Journal* 14: 7–92.
- Millspaugh, C.F. (1889) Contributions to North American Euphorbiaceae. *Proceedings of the California Academy of Sciences, Series 2*, 2: 217–230.
- Milne-Redhead, E.W.B.H. (1937) *Phyllanthus holostylus* in Tropical African Plants XVII. *Bulletin of Miscellaneous Information, Kew* 1937: 414.
<https://doi.org/10.2307/4107099>
- Miquel, F.A.W. (1848) Symbolae ad Floram Surinamensem. *Linnaea* 21: 473–479.
- Miquel, F.A.W. (1859) *Flora van Nederlandsch Indië* 1 (2). C.G. van der Post, Amsterdam, 704 pp.
- Miquel, F.A.W. (1861) Overzicht der thans bekende Flora van Sumatera. In: *Flora van Nederlandsch Indië, Eerste Bijvoegsel*. 104–276. C.G. van der Post, Amsterdam.
- Mitchell, T.L. (1848) *Journal of an expedition into the interior of tropical Australia, in search of a route from Sydney to the Gulf of Carpentaria*. Longman, Brown, Green and Longmans, London, 437 pp.
- Mitra, R.L. & Sanjappa, M. (2003) *Phyllanthus parvifolius*, *P. clarkei* (Euphorbiaceae) and related Indian taxa. *Bulletin of the Botanical Survey of India* 45: 1–20.
- Mohanan, M. (1985) Notes on the nomenclature of some Indian plants. *Journal of Economic and Taxonomic Botany* 6: 480.
- Moore, J.W. (1933) New and critical plants from Raiatea. *Bernice P. Bishop Museum Bulletin* 102: 1–53.
- Moore, J.W. (1940) New species of dicotyledonous spermatophytes from Tahiti. *Occasional Papers of the Bernice Pauahi Bishop Museum of Polynesian Ethology and Natural History* 16: 1–24.
- Moore, J.W. (1963) Notes on Raiatean flowering plants, with descriptions of new species and varieties. *Bernice P. Bishop Museum Bulletin* 226: 1–36.
- Moore, S.L.M. (1905) *Alabastra diversae*. Part XII. *Journal of Botany, British and Foreign* 43: 137–149.
- Moore, S.L.M. (1911) Monochlamydeae. In: Rendle *et al.* (Eds.) A contribution to our knowledge of the Flora of Gazaland: being an account of collections made by C.F.M. Swynnerton, F.L.S. *The Journal of the Linnean Society, Botany* 40: 181–206.
<https://doi.org/10.1111/j.1095-8339.1911.tb00872.x>
- Moore, S.L.M. (1920) A contribution to the flora of Australia. *The Journal of the Linnean Society, Botany* 45: 159–221.
<https://doi.org/10.1111/j.1095-8339.1920.tb00123.x>
- Moore, S.L.M. (1921) Monochlamydeae. In: Rendle, A.B., Moore, S., Baker, E.G. & Gepp, A. (eds.) A systematic account of the Plants collected in New Caledonia and the Isle of Pines by Prof. R.H. Compton, M.A. in 1914. – Part I. Flowering Plants (Angiosperms). *The Journal of the Linnean Society, Botany* 45: 245–417.
<https://doi.org/10.1111/j.1095-8339.1921.tb00125.x>
- Moore, S.L.M. (1923) Dr. H.O. Forbe's New Guinea Plants. *Journal of Botany, British and Foreign* 61 supplementum: 1–64.
- Moore, S.L.M. (1926) Euphorbiaceae. In: Rendle, A.B., Moore, S., Baker, E.G. & Gepp, A. (Eds.) Capt. G. H. Wilkins's Groote Eylandt Plants. *Journal of Botany* 64: 89–99.
- Morong, T. & Britton, N.L. (1892) An enumeration of the plants collected by Dr. Thomas Morong in Paraguay, 1888–1890. *Annals of the New York Academy of Sciences* 7: 45–280.
<https://doi.org/10.1111/j.1749-6632.1893.tb55410.x>
- Mueller, F.J.H. von (1853) Diagnoses et descriptiones plantarum novarum, quas in Nova Hollandia australi praecipue in regionibus interioribus. *Linnaea* 25: 367–445.

- Mueller, F.J.H. von (1855) Definitions of rare or hitherto undescribed Australian plants, chiefly collected within the boundaries of the Colony of Victoria and examined by Dr. Ferd. Mueller. *Transactions of the Philosophical Society of Victoria* 1: 5–24.
- Mueller, F.J.H. von (1859) *Fragmenta phytographiae australiae* 1. Government Printer, Melbourne, 252 pp.
<https://doi.org/10.5962/bhl.title.116758>
- Mueller, F.J.H. (1876) von *Fragmenta phytographiae australiae* 10. Government Printer, Melbourne, 145 pp.
- Mueller, F.J.H. von (1892) Descriptions of new Australian plants, with occasional other annotations. *Victorian Naturalist* 7: 177–180.
- Müller (Argoviensis), J. (1863) Euphorbiaceae: Vorläufige Mittheilungen aus dem für De Candolle's Prodrusus bestimmten Manuscript über diese Familie. *Linnaea* 32: 1–126.
- Müller (Argovensis), J. (1864) Euphorbiaceae novae a C. Dr. Welwitsch in Africa Aequinoctiali Occidentali Lectae. *Journal of Botany* 2: 327–339.
- Müller (Argovensis), J. (1865a) Ueber Glochidion (Forst). *Flora* 48: 369–390.
- Müller (Argovensis) J. (1865b) Euphorbiaceae: Vorläufige Mittheilungen aus dem für De Candolle's Prodrusus bestimmten Manuscript über diese Familie. *Linnaea* 34: 1–224.
- Müller (Argovensis), J. (1866) Euphorbiaceae excl. Euphorbiae. In: De Candolle, A.L.P.P. de (Ed.) *Prodromus Systematis Naturalis Regni Vegetabilis* 15,2. Victoris Masson et Filii, Parisiis, pp. 190–1260.
- Müller (Argoviensis), J. (1873) Euphorbiaceae. In: Martius CFP von & Eichler, A.W. (Eds.) *Flora Brasiliensis* 11 (2). R. Oldenbourg, Munich & Leipzig, pp. 1–292.
- Müller (Argoviensis), J. (1880) Euphorbiaceae. In: Buchenau, F., Reliquiae Rutenbergianae I (Botanik, Taf. I, II). *Abhandlungen herausgegeben vom Naturwissenschaftlichen Vereine zu Bremen* 7: 24–30.
- Murugan, C., Kabeer, K.A.A. & Murthy, G.V.S. (2009) *Phyllanthus rangachariarii*—A new species of Euphorbiaceae from Agasthyiamalai, India. *Bulletin of the Botanical Survey of India* 50: 201–203.
- Nadeaud, J. (1873) *Énumération des Plantes Indigènes de l'Île de Tahiti*. F. Savy, Paris, 86 pp.
- Naudin, C.V. (1845) Additions a la Flore du Brésil Méridional. *Annales des Sciences Naturelles, Botanique, sér.* 3, 3: 168–192.
- Nuttall, T. (1837) Collections towards a Flora of the Territory of Arkansas. *Transactions of the American Philosophical Society, new series* 5 (6,2): 139–204.
<https://doi.org/10.2307/1004943>
- Orlandini, P., Cordeiro, I., Campos-Rocha, A. & Souza, V.C. (2020) A new species of *Phyllanthus* L. (Phyllanthaceae) with phylloclades from Minas Gerais, Brazil. *Phytotaxa* 455: 167–172.
<https://doi.org/10.11646/phytotaxa.455.2.8>
- Orlandini, P., Cordeiro, I., Mendes, J.C.R., Campos-Rocha, A. & Souza, V.C. (2021) A New Species of Phyllocladiferous *Phyllanthus* (Phyllanthaceae) from the Atlantic Rain Forest. *Systematic Botany* 46 (4): 1011–1015.
- Orlandini, P., Cordeiro, I., José da Silva, M., Athiê-Souza, S.M. (2022) *Phyllanthus chapadensis*, a new phyllocladiferous *Phyllanthus* (Phyllanthaceae) from the Chapada dos Veadeiros, Goiás, Brazil. *Phytotaxa* 532 (2): 169–175.
<https://doi.org/10.11646/phytotaxa.532.2.5>
- Parodi, D. (1881) Diez nuevas especies pertenecientes á la familia de las Euphorbiáceas. *Anales de la Sociedad Científica Argentina* 11: 49–56.
- Pax, F. (1890) Euphorbiaceae. In: Engler, H.G.A. & Prantl, K.A.E. (Eds.) *Die Natürlichen Pflanzenfamilien* 3 (5). Wilhelm Engelmann, Leipzig, pp. 1–119.
- Pax, F. (1893) Euphorbiaceae africanae I (Phyllanthoideae et Crotonae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 15: 522–535.
- Pax, F. (1894) Euphorbiaceae africanae II. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 19: 76–127.
- Pax, F. (1895) Euphorbiaceae. In: Engler, H.G.A. (Ed.) *Die Pflanzenwelt Ost-Afrikas* C. D. Reimer, Berlin, pp. 235–243.
- Pax, F. (1898) Euphorbiaceae. In: Reinecke, F., *Die Flora der Samoa-Inseln* II. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 25: 644–649.
- Pax, F. (1899) Euphorbiaceae africanae V. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 28: 18–27.
- Pax, F. (1909a) Euphorbiaceae africanae IX. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 43: 75–90.
- Pax, F. (1909b) Beiträge zur Flora von Afrika XXXV. Euphorbiaceae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 43: 317–325.
- Pax, F. (1910) Euphorbiaceae africanae XI. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 45: 234–241.
- Pax, F. (1923) Euphorbiaceae americanae novae. I. *Repertorium Specierum Novarum Regni Vegetabilis* 19: 174–177.

<https://doi.org/10.1002/fedr.19230191104>

- Pax, F. & Hoffmann, K. (1911) Euphorbiaceae—Cluytieae. *In*: Engler, H.G.A., *Das Pflanzenreich* IV.147.iii (Heft 47). Wilhelm Engelmann, Leipzig, pp. 1–124
- Pax, F. & Hoffmann, K. (1921) Euphorbiaceae—Phyllanthoideae—Phyllanthaceae. *In*: Engler, A. & Drude, O. (eds.) *Die Vegetation der Erde 9: Die Pflanzenwelt Afrikas* 3. Wilhelm Engelmann, Leipzig, pp. 11–232.
- Pax, F. & Hoffmann, K. (1922) Euphorbiaceae—Phyllanthoideae—Phyllanthaceae—Wielandiinae. *In*: Engler, H.G.A. (ed.) *Das Pflanzenreich* IV.147.xv (Heft 81). Wilhelm Engelmann, Leipzig, pp. 180–189.
- Pax, F. & Hoffmann, K. (1931) Euphorbiaceae. *In*: Engler, A. & Harms, H. (Eds.) *Die natürlichen Pflanzenfamilien ed. 2*, 19c. Wilhelm Engelmann, Leipzig, pp. 11–232.
- Pelser, P.B., Barcelona, J.F. & Nickrent, D.L.(eds.) (2011 onwards) Co's Digital Flora of the Philippines. www.philippineplants.org
- Person, C.H. (1807) *Synopsis plantarum* 2 (2). C.F. Cramer, Paris & J.G. Cotta, Tübingen, pp. 273–657.
- Pornpongrueng, P., Parnell, J.A., Hodkinson, T.R. & Chantaranonthai, P. (2017) *Phyllanthus kaweesakii* (Phyllanthaceae), a new species from Thailand. *Botany* 95: 567–577.
<https://doi.org/10.1139/cjb-2016-0298>
- Pornpongrueng, P., Chantaranonthai, P., Parnell, J.A. & Hodkinson, T.R. (2019) Two new species of *Phyllanthus* (Phyllanthaceae) from Thailand. *PhytoKeys* 136: 35–44.
<https://doi.org/10.3897/phytokeys.136.47625>
- Post, T.E. & Kuntze, O. (1903) *Lexikon generum phanerogamarum*. Deutsche Verlags-Anstalt, Stuttgart, 714 pp.
- Punt, W. (1967) Pollen morphology of the genus *Phyllanthus* (Euphorbiaceae). *Review of Palaeobotany and Palynology* 3: 141–150.
[https://doi.org/10.1016/0034-6667\(67\)90047-4](https://doi.org/10.1016/0034-6667(67)90047-4)
- Punt, W. (1972) Pollen morphology and taxonomy of section *Ceramanthus* Baillon s.l. of the genus *Phyllanthus* (Euphorbiaceae). *Review of Palaeobotany and Palynology* 13: 213–228.
[https://doi.org/10.1016/0034-6667\(72\)90031-0](https://doi.org/10.1016/0034-6667(72)90031-0)
- Punt, W. (1980) Pollen morphology of the *Phyllanthus* species (Euphorbiaceae) occurring in New Guinea. *Review of Palaeobotany and Palynology* 31: 155–177.
[https://doi.org/10.1016/0034-6667\(80\)90025-1](https://doi.org/10.1016/0034-6667(80)90025-1)
- Punt, W. (1986) Convergence in some interesting pollen types of *Phyllanthus* (Euphorbiaceae). *Canadian Journal of Botany* 64: 3127–3129.
<https://doi.org/10.1139/b86-411>
- Punt, W. (1987) A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. *Botanical Journal of the Linnean Society* 94: 127–142.
<https://doi.org/10.1111/j.1095-8339.1987.tb01042.x>
- Quisumbing, E. & Merrill, E.D. (1928) New Philippine plants. *The Philippine Journal of Science* 37: 1–212.
- Radcliffe-Smith, A. (1974) Notes on African Euphorbiaceae: V. *Kew Bulletin* 29: 435–441.
<https://doi.org/10.2307/4108554>
- Radcliffe-Smith, A. (1981) Notes on African Euphorbiaceae: IX. *Kew Bulletin* 35: 763–777.
<https://doi.org/10.2307/4110172>
- Radcliffe-Smith, A. (1982) Notes on African Euphorbiaceae: XII. *Kew Bulletin* 37: 421–428.
<https://doi.org/10.2307/4110042>
- Radcliffe-Smith, A. (1992) Notes on African Euphorbiaceae XXVIII. *Kew Bulletin* 47: 677–683.
<https://doi.org/10.2307/4110706>
- Radcliffe-Smith, A. (1996) Euphorbiaceae. *In*: Pope, G.V. (Ed.) *Flora Zambesiaca* 9 (4). Royal Botanical Gardens, Kew, London, 377 pp.
- Radcliffe-Smith, A. (2001) *Genera Euphorbiacearum*. Royal Botanic Gardens, Kew, 261 pp.
- Radcliffe-Smith, A. & Hoffmann, P. (2006) New records, names and combinations in African Euphorbiaceae sensu lato. *Kew Bulletin* 61: 609–611.
- Rafinesque, C.S. (1821) *Western Minerva*. Published by T. Smith for the author, Lexington, Kentucky, 88 pp.
- Rafinesque, C.S. (1825) *Neogenyton*. Lexington, Notre Dame, 4 pp.
- Rafinesque, C.S. (1838) *Sylva Telluriana*. Published by the author, Philadelphia, 184 pp.
- Raizada, M.B. & Bennet, S.S.R. (1983) Six new names and two new combinations for flowering plants. *Indian Forester* 109: 219–221.
- Raja Kullayiswamy, K., Sarojini Devi, N. & Karanth, K.P. (2021) *Phyllanthus palakondensis* sp. nov. (Phyllanthaceae) from Eastern Ghats of Andhra Pradesh, India. *Nordic Journal of Botany* 39 (11): 1–6.
- Ralimanana, H. & Hoffmann, P. (2011) Taxonomic revision of *Phyllanthus* (Phyllanthaceae) in Madagascar and the Comoro Islands I: synopsis and subgenera *Isocladius*, *Betsileani*, *Kirganelia* and *Tenellanthus*. *Kew Bulletin* 66: 331–365.

<https://doi.org/10.1007/s12225-011-9294-8>

- Ralimanana, H. & Hoffmann, P. (2014) Taxonomic revision of *Phyllanthus* L. (Phyllanthaceae) in Madagascar and the Comoro Islands II: subgenera *Anisonemoides* (Jean F. Brunel) Ralim. & Petra Hoffm., stat. nov. and *Menarda* (Müll. Arg.) Ralim. & Petra Hoffm., stat. nov. *Adansonia sér.* 3, 36: 265–301.
<https://doi.org/10.5252/a2014n2a9>
- Ralimanana, H., Hoffmann, P. & Rajeriarison, C. (2013) Taxonomic revision of *Phyllanthus* (Phyllanthaceae) in Madagascar and the Comoro Islands III: subgenera *Swartziani*, *Afroswartziani* and *Emblica*. *Kew Bulletin* 68: 535–558.
<https://doi.org/10.1007/s12225-013-9485-6>
- Ralimanana, H. & Cable, S. (2020) Taxonomic revision of *Phyllanthus* (Phyllanthaceae) in Madagascar and the Comoro Islands IV: subgenus *Anisonemoides* section *Pseudogomphidium* and incertae sedis. *Kew Bulletin* 75 (4): 1–21.
- Rehder, A. (1933) Notes on the ligneous plants described by Lévillé from Eastern Asia. *Journal of the Arnold Arboretum* 14: 223–252.
- Rehder, A. (1937) Notes on the ligneous plants described by H. Lévillé from Eastern Asia. *Journal of the Arnold Arboretum* 18: 206–257.
<https://doi.org/10.5962/p.185369>
- Retzius, A.J. (1789) *Observationes botanicae: sex fasciculis comprehensae*. Siegfried Lebrecht Crusium, Lipsiae, 67 pp.
- Ribeiro, R.T.M., Neto, R.L.S. & Loiola, M.I.B. (2017) *Phyllanthus carmenluciae*, a supreme species of *Phyllanthus* (Phyllanthaceae) from Brazil. *Phytotaxa* 305: 35–40.
<https://doi.org/10.11646/phytotaxa.305.1.5>
- Richard, A. (1850) Euphorbiaceae. In: Sagra, R. de La, *Historia Física Política y Natural de la Isla de Cuba*. Botánica 11: 195–218.
- Richard, L.C.M. (1792) Catalogus Plantarum ad Societatem, ineunte anno 1792, e Cayenna missarum à Domino le Blond. *Actes de la Société d'Histoire Naturelle de Paris* 1: 105–114.
- Richard, L.C.M. (1807) Commentatio de *Convallaria japonica*, novum genus constituenta. Praemissis nonnullis circa plantas Liliaceae observationibus. *Neues Journal für die Botanik* 2: 1–10.
- Richard, L.C.M. (1808) *Demonstrations Botaniques: Ou Analyse Du Fruit Consideré en General*. Chez Gabon, Paris, 127 pp.
- Ridley, H.N. (1893) On the flora of the Eastern Coast of the Malay Peninsula. *Transactions of the Linnean Society of London, 2nd series, Botany* 3: 267–409.
<https://doi.org/10.1111/j.1095-8339.1893.tb00678.x>
- Ridley, H.N. (1909) The flora of the Telom and Batang Padang Valleys. *Journal of the Federated Malay States Museums* 4: 1–98.
- Ridley, H.N. (1911) An account of a botanical expeditions to Lower Siam. *Journal of the Straits Branch of the Royal Asiatic Society* 59: 27–234.
- Ridley, H.N. (1923) New Euphorbiaceae from the Malay Peninsula. *Bulletin of Miscellaneous Information Kew* 1923: 360–369.
<https://doi.org/10.2307/4115416>
- Ridley, H.N. (1924) *The Flora of the Malay Peninsula* 3. L. Reeve & Co, London, 405 pp.
- Riley, L.A.M. (1926) Notes on the Flora of Rapa. *Bulletin of Miscellaneous Information Kew* 1926: 51–56.
<https://doi.org/10.2307/4107500>
- Robinson, B.L. & Greenman, J.M. (1894) Further new and imperfectly known plants collected in Mexico by C.G. Pringle in the summer of 1893. *Proceedings of the American Academy of Arts and Sciences* 29: 382–394.
<https://doi.org/10.2307/20020566>
- Robinson, C.B. (1909) Philippine Phyllanthinae. *The Philippine Journal of Science, Section C, Botany* 4: 71–105.
- Robinson, C.B. (1911) Alabastra Philippensia, III. *The Philippine Journal of Science, Section C, Botany* 6: 319–358.
- Robyns, F.H.E.A.W. & Lawalrée, A.G.C. (1947) Euphorbiaceae. In: Robyns, F.H.E.A.W. (Ed.) Choripétales nouvelles de la région du Parc National Albert (Congo Belge). *Bulletin du Jardin Botanique de l'État à Bruxelles* 18: 261–292.
<https://doi.org/10.2307/3666560>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Rossignol, L., Rossignol, M. & Haicour, R. (1987) A systematic revision of *Phyllanthus* subsection *Urinaria* (Euphorbiaceae). *American Journal of Botany* 74: 1853–1862.
<https://doi.org/10.1002/j.1537-2197.1987.tb08787.x>
- Roxburgh, W. (1832) *Flora Indica ed. 1832*, 3 W. Thacker and Co., Calcutta, pp. 1–875.
- Ruprecht, F.J.I. & Maximowicz, C.J. (1857) Die ersten botanischen Nachrichten über das Amurland. *Bulletin de la Classe physico-mathématique de l'Académie impériale des sciences de Saint-Petersbourg* 15: 209–238.
- Rusby, H.H. (1912) New species from Bolivia, collected by R.S. Williams—II. *Bulletin of the New York Botanical Garden* 8 (28): 89–

- Sagun, V.G. & Van Der Ham, R.W.M. (2003) Pollen morphology of the Flueggeinae (Euphorbiaceae, Phyllanthoideae). *Grana* 42: 193–219.
<https://doi.org/10.1080/00173130310016464>
- Santiago, L.J.M. (1988) Estudos preliminares da seção *Choretropsis* Muell. Arg., gênero *Phyllanthus* L. (Euphorbiaceae). *Bradea* 5: 44–49.
- Santiago, L.J.M., Louro, R.P. & Emmerich, M. (2006) *Phyllanthus* section *Choretropsis* (Euphorbiaceae) in Brazil. *The Botanical Journal of the Linnean Society* 150: 131–164.
<https://doi.org/10.1111/j.1095-8339.2006.00459.x>
- Schlechter, F.R.R. (1906) Beiträge zur Kenntnis der Flora von Neu-Kaledonien. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 39: 1–274.
- Schmid, M. (1991) *Phyllanthus*. In: McPherson, G. & Schmid, M. (eds.) *Flore de la Nouvelle-Calédonie et Dépendances* 17. Association de Botanique Tropicale, Paris, pp. 31–324.
- Schultz, C.F. (1806) *Prodromus Florae Stargardiensis*. Sumtibus C.F.E. Spaethen, Berolini, 531 pp.
- Schumacher, H.C.F. & Thonning, P. (1827) *Phyllanthus*. In: Schumacher, H.C.F., *Beskrivelse af Guineeske Planter*. H.F. Popp, Kjöbenhavn, 466 pp. (415–423).
- Schumann, K.M. (1887) Die Flora der deutschen ost-asiatischen Schutzgebiete. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 9: 189–224.
- Schumann, K.M. (1905) Euphorbiaceae. In: Schumann, K.M. & Lauterbach, C.A.G., *Nachträge zur Flora der deutschen Schutzgebiete in der Südsee (mit Ausschluss Samoa's und der Karolinen)*. Gebrüder Borntraeger, Leipzig, pp. 285–300.
<https://doi.org/10.5962/bhl.title.710>
- Schumann, K.M. & Lauterbach, C.A.G. (1900) *Die Flora der deutschen Schutzgebiete in der Südsee*. Gebrüder Borntraeger, Leipzig, 606 pp.
- Schweigger, A.F. (1812) *Enumeratio plantarum horti botanici Regiomontani*. Typis Academicis, Regiomonti [Königsberg], 82 pp.
- Schweinfurth, G.A. (1899) Sammlung Arabisch-aethiopischer Pflanzen. *Bulletin de l'Herbier Boissier* 7, Appendix 2: 267–340.
- Sebastine, K.M. & Henry, A.N. (1960) A new species of *Reidia* from South India. *Bulletin of the Botanical Survey of India* 2: 437–439.
- Secco, R. da S. & Rosário, A.S. de (2015) A new species of *Phyllanthus* (Phyllanthaceae) endemic to Amazonas State, Brazil. *Novon* 24: 209–211.
<https://doi.org/10.3417/2013025>
- Sedgwick, L.J. (1921) New Bombay species. *Journal of Indian Botany* 2: 123–132.
- Siebold, P.F.(B.) & Zuccarini, J.G. (1845) Florae Japonicae familiae naturales, adjectis generum et specierum exemplis selectis. Sectio prima. Plantae dicotyledoneae Polypetalae auctoribus. *Abhandlungen der Mathematisch-Physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften* 4 (2): 109–204.
<https://doi.org/10.5962/bhl.title.10718>
- Silva, M.J. (2009) Two new Brazilian species of *Phyllanthus* (Phyllanthaceae). *Novon* 19: 229–233.
<https://doi.org/10.3417/2008022>
- Silva, M.J. & Sales, M.F. (2006) A new species of *Phyllanthus* (Phyllanthaceae) from northeastern Brazil. *Novon* 16: 421–423.
[https://doi.org/10.3417/1055-3177\(2006\)16\[421:ANSOPP\]2.0.CO;2](https://doi.org/10.3417/1055-3177(2006)16[421:ANSOPP]2.0.CO;2)
- Skeels, H.C. (1909) Seeds and plants imported during the period from July 1 to September 30, 1908: Inventory no. 16; NOS 23323 to 23744. *U.S. Department of Agriculture Bureau of Plant Industry Bulletin* 148: 1–37.
- Small, J.K. (1913) Euphorbiaceae. In: Britton, N.L. & Brown, A. (Eds.) *An illustrated flora of the Northern United States ed. 2*, 2. Charles Scribner's Sons, New York, pp. 452–477.
- Smith, A.C. (1952) Studies of Pacific Island Plants XIII. Notes on Fijian Euphorbiaceae. *Journal of the Arnold Arboretum* 33: 367–403.
- Smith, A.C. (1967) Studies of Pacific Island Plants, XVIII: New and noteworthy flowering plants from Fiji. *Contributions from the United States National Herbarium* 37: 69–106.
- Smith, A.C. (1981) *Flora Vitiensis Nova* 2. Lawaii, Kauai, 810 pp.
- Smith, J.J. (1908) Tab CCLXIII. *Phyllanthus tenuirhachis*. *Icones Bogorienses* 3: 160–163.
- Smith, J.J. (1910) Euphorbiaceae. In: Koorders, S.H. & Valetton, T. (Eds.) Bijdrage no. 12 tot de kennis der boomsoorten op Java. *Mededeelingen uitgaande van het Departement van Landbouw* 10. G. Kolff & Co., Batavia, pp. 9–638.
- Smith, J.J. (1912) Euphorbiaceae. In: Lorentz, M.H.A. (ed.) *Nova Guinea* 8 (2): 779–796.
- Smith, J.J. (1917) Euphorbiaceae. *Nova Guinea* 12: 543–548.
<https://doi.org/10.1177/002205741708602006>
- Smith, J.J. (1920) Plantae novae vel criticae ex Herbario et Horto Bogoriensi. I. *Bulletin du Jardin Botanique de Buitenzorg ser. 3*, 1: 390–410.

- Smith, W.W. (1914) Diagnoses specierum novarum in herbario Horti Regii Botanici Edinburgensis cognitarum (Species chinenses). *Notes from the Royal Botanic Garden, Edinburgh* 8 (38): 173–212.
- Smith, W.W. (1921) Diagnoses specierum novarum in herbario Horti Regii Botanici Edinburgensis cognitarum. *Notes from the Royal Botanic Garden, Edinburgh* 13: 149–187.
- Sonder, O.W. (1850) Beiträge zur Flora von Südafrika. *Linnaea* 23: 1–138.
- Spanoghe, J.B. (1841) Prodrromus Florae Timorensis. *Linnaea* 15: 161–313.
- Sprague, T.A. (1909) Decades kewenses LII–LIII. *Bulletin of Miscellaneous Information Kew* 1909: 256–268.
<https://doi.org/10.2307/4111513>
- Sprengel, K.P.J. (1826) *Systema Vegetabilium ed. 16*, 3. Sumtibus Librariae Dieterichianae, Gottingae, 936 pp.
- St. John, H. & Philipson, W.R. (1962) An account of the Flora of Henderson Island, South Pacific Ocean. *Transactions of the Royal Society of New Zealand* 1: 1–20.
- Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
<https://doi.org/10.1093/bioinformatics/btu033>
- Standley, P.C. (1937) Euphorbiaceae. In: Standley, P.C. (Ed.) Flora of Costa Rica part II. *Publications of the Field Museum of Natural History, Botanical Series* 18 (2): 598–622.
- Standley, P.C. (1940) Euphorbiaceae. In: Standley, P.C. & Steyermark, J.A. (Eds.) Studies of Central American Plants II. *Publications of the Field Museum of Natural History, Botanical Series* 22 (5): 346–347.
- Standley, P.C. (1948) Euphorbiaceae. In: Leavenworth, W.C., A preliminary study of the vegetation of the region between Cerro Tancitaro and the Rio Tepalcatepec, Michoacan, Mexico. *American Midland Naturalist* 36: 176–178.
- Standley, P.C. & Steyermark, J.A. (1944) Studies of Central American Plants V. *Publications of the Field Museum of Natural History, Botanical Series* 23 (3): 113–150.
- Stapf, O. (1905) Contributions to the Flora of Liberia. *The Journal of the Linnean Society, Botany* 37: 79–115.
<https://doi.org/10.1111/j.1095-8339.1905.tb00826.x>
- Steyermark, J.A. (1952) Botanical Exploration in Venezuela—II; from Droseraceae through Umbelliferae. *Fieldiana, Botany* 28: 243–447.
- Steyermark, J.A. (1958) The Machris Brazilian Expedition. Botany: Phanerogamae, Euphorbiaceae, Lentibulariaceae, and Rubiaceae. *Los Angeles County Museum Contributions in Science* 21: 3–31.
<https://doi.org/10.5962/p.214235>
- Steyermark, J.A. (1975, publ. 1976) Novedades Venezolanas. *Acta Botanica Venezuelica* 10: 235–246.
- Steyermark, J.A. & Brewer-Carias, C. (1976) La vegetación de la cima del Macizo de Jaua. *Boletín de la Sociedad Venezolana de Ciencias Naturales* 32 (132–133): 179–406.
- Steyermark, J.A. & Luteyn, J.L. (1984) Flora of the Venezuelan Guayana—I. *Annals of the Missouri Botanical Garden* 71: 297–340.
<https://doi.org/10.2307/2399074>
- Stokes, J.S. (1812) *A Botanical Materia Medica* 4. J. Johnson & Co., London, pp. 1–702.
- Sunil, C.N., Prabhukumar, K.M., Kumar, V.V.N., Thomas, V.P., Bhavadas, N. & Balachandran, I. (2016) *Phyllanthus balakrishnanii* sp. nov. (Phyllanthaceae), an interesting discovery from the southern Western Ghats, India. *Phytotaxa* 273: 65–71.
<https://doi.org/10.11646/phytotaxa.273.1.7>
- Swartz, O. (1788) *Nova genera & species plantarum seu Prodrromus*. M. Sweder, Stockholm, Uppsala & Åbo, 158 pp.
- Swartz, O. (1791) *Observationes botanicae*. Jo. Jacobus Palm, Erlangen, 424 pp.
- Swartz, O. (1800) *Flora Indiae Occidentalis* 2 (2). Jo. Jacobus Palm, Erlangen, pp. 929–1230.
- Swofford, D. (2002) PAUP*, version 4 beta 10. Software distributed by Sinauer Associates, Sunderland, Massachusetts.
- Tagane, S., Toyama, H., Chhang, P., Nagamasu, H. & Yahara, T. (2015) Flora of Bokor National Park, Cambodia I: Thirteen new species and one change in status. *Acta Phytotaxonomica et Geobotanica* 66: 95–135.
- The Plant List (2013) *The Plant List Version 1.1*. Published on the Internet; <http://www.theplantlist.org/> (accessed March 2019).
- Telford, I.R.H. & Naaykens, J. (2015) *Synostemon hamersleyensis* (Phyllanthaceae), a new species endemic to the Pilbara, Western Australia. *Nuytsia* 25: 32–36.
- Telford, I.R.H., Pruesapan, K., van Welzen, P.C. & Bruhl, J.J. (2015) Molecular data consistently recover a “Queensland clade” of *Synostemon* (Phyllanthaceae, Phyllanthae) with distinctive floral morphology. *Australian Systematic Botany* 27: 450–461.
<https://doi.org/10.1071/SB14034>
- Telford, I.R.H., Pruesapan, K., van Welzen, P.C. & Bruhl, J.J. (2016) Morphological and molecular data show *Synostemon trachyspermus* (Phyllanthaceae, Phyllanthae) to be a heterogeneous species assemblage. *Australian Systematic Botany* 29: 218–234.
<https://doi.org/10.1071/SB16008>
- Telford, I.R.H., Pruesapan, K., van Welzen, P.C. & Bruhl, J.J. (2019) Morphological and molecular data show an enlarged tropical radiation

- in *Synostemon* (Phyllanthaceae, Phyllanthaeae) previously concealed by heteromorphic species concepts. *Australian Systematic Botany* 32: 146–176.
<https://doi.org/10.1071/SB18029>
- Thin, N.N. (1992) Some new species of genera: *Phyllanthus* and *Sauropus* for the flora of Vietnam. *Journal of Biology* (Hanoi) 14 (2): 16–25.
- Thin, N.N. (1995) *Euphorbiaceae of Vietnam*. Agriculture Publ. House, Hanoi, 50 pp.
- Thin, N.N. (1999) *Key to taxa and taxonomy of Euphorbiaceae in Vietnam*. Agriculture Publ. House, Hanoi, 138 pp.
- Thin, N.N. (2007) Taxonomy of Euphorbiaceae in Vietnam. National University Publishers, Hanoi, 407 pp.
- Thulin, M. (2003) *Phyllanthus xylorrhizus* (Phyllanthaceae), a new species from Somalia. *Nordic Journal of Botany* 23: 385–387.
<https://doi.org/10.1111/j.1756-1051.2003.tb00409.x>
- Thunberg, C.P. (1794) *Prodrum plantarum Capensium* 1. J. Edman, Upsala, 83 pp.
- Thunberg, C.P. (1817) *Plantarum Brasiliensium* 1. Typis Zeipel et Palmblad, Upsala, 15 pp.
- Thwaites, G.H.K. & Hooker, J.D. (1861) *Enumeratio Plantarum Zeylanicae*. Dulau & Co., London, 483 pp.
- Torrey, J. (1859) General Botany. In: Emory, W.H. (ed., *Report on the United States and Mexican boundary survey*. C. Wendell, Washington, pp. 28–270.
- Trimen, H. (1885) Notes on the Flora of Ceylon. *Journal of Botany, British and Foreign* 23: 238–247.
- Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Koeltz Botanical Books.
<https://doi.org/10.12705/Code.2018>
- Urban, I. (1902) Nova genera et species II. *Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis* 3 (2). Gebrüder Borntraeger, Leipzig *et al.*, pp. 280–352.
- Urban, I. (1908) Nova genera et species III. *Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis* 5 (3). Gebrüder Borntraeger, Leipzig *et al.*, pp. 353–532.
- Urban, I. (1909) Nova genera et species IV. *Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis* 6 (1). Gebrüder Borntraeger, Leipzig *et al.*, pp. 1–55.
- Urban, I. (1912) Nova genera et species V. *Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis* 7 (2). Gebrüder Borntraeger, Leipzig *et al.*, pp. 161–304.
- Urban, I. (1914) Sertum antillanum I. *Repertorium Specierum Novarum Regni Vegetabilis* 13: 444–459.
<https://doi.org/10.1002/fedr.19140132708>
- Urban, I. (1919) Sertum antillanum IV. *Repertorium Specierum Novarum Regni Vegetabilis* 15: 397–415.
<https://doi.org/10.1002/fedr.19190152505>
- Urban, I. (1921) Plantae Haitienses novae vel rariores a cl. Er. L. Ekman 1917 lectae. *Arkiv för Botanik* 17: 1–72.
- Urban, I. (1924) Plantae cubense novae vel rariores II. *Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis* 9 (2). Gebrüder Borntraeger, Leipzig *et al.*, pp. 177–272.
- Urban, I. (1928) Plantae Haitienses et Domingenses novae vel rariores V a cl. E. L. Ekman 1924–1927 lectae. *Arkiv för Botanik* 22: 1–106.
- Urban, I. (1930) Sertum antillanum XXX. *Repertorium Specierum Novarum Regni Vegetabilis* 28: 209–235.
<https://doi.org/10.1002/fedr.4870281402>
- Vahl, M. (1791) *Symbolae botanicae* 2. Impensis auctoris, excudebant N. Möller et filius, Hauniae [Copenhagen], 108 pp.
- van Welzen, P.C. (2000) The distichous Euphorbiaceae genera of Thailand. *Thai Forest Bulletin (Botany)* 28: 51–58.
- van Welzen, P.C. (2017) Reduction of *Breynia* subgenus *Hemisauropus* to *B.* section *Cryptogynium* and discussion of the *B. quadrangularis* complex (Phyllanthaceae). *Blumea* 62: 90–91.
<https://doi.org/10.3767/blumea.2017.62.02.02>
- van Welzen, P.C., Haegens, R.M., Slik, J.W., Bollendorff, S.M., Dressler, S. & Esser, H.-J. (2014) Checklist of the genera of Thai Euphorbiaceae—I. *Thai Forest Bulletin (Botany)* 28: 59–111.
- van Welzen, P.C., Pruesapan, K., Telford, I.R.H., Esser, H.-J. & Bruhl, J.J. (2014) Phylogenetic reconstruction prompts taxonomic changes in *Sauropus*, *Synostemon* and *Breynia* (Phyllanthaceae tribe Phyllanthaeae). *Blumea* 59: 77–94.
<https://doi.org/10.3767/000651914X684484>
- Vellozo, J.M. da C. (1831) *Florae Fluminensis*. Ex Typographia Nationali, Rio de Janeiro, 1640 pl.
- Verwijns, J.I.M., Bouman, R.W. & van Welzen, P.C. (2019) A taxonomic revision of *Phyllanthus* subgenus *Macraea* (Phyllanthaceae). *Blumea* 64: 231–252.
<https://doi.org/10.3767/blumea.2019.64.03.05>

- Wagner, W.L. & Lorence, D.H. (2011) A nomenclator of Pacific oceanic island *Phyllanthus* (Phyllanthaceae), including *Glochidion*. *PhytoKeys* 4: 67–94.
<https://doi.org/10.3897/phytokeys.4.1581>
- Walpers, W.G. (1852) *Annales Botanices Systematicae* 3. F. Hofmeister, Leipzig, pp. 1–1168.
- Walter, T. (1788) *Flora caroliniana*. J. Fraser, London, 263 pp.
- Warburg, O. (1891) Beiträge zur Kenntnis der papuanischen Flora. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 13: 230–455.
- Warburg, O. (1894) Plantae Hellwigianae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 18: 184–212.
- Webster, G.L. (1955) Studies of the Euphorbiaceae, Phyllanthoideae I. Taxonomic notes on the West Indian species of *Phyllanthus*. *Contributions from the Gray Herbarium of Harvard University* 176: 44–63.
- Webster, G.L. (1956) A monographic study of the West Indian species of *Phyllanthus*. *Journal of the Arnold Arboretum* 37: 91–122.
<https://doi.org/10.5962/p.324651>
- Webster, G.L. (1957) A monographic study of the West Indian species of *Phyllanthus*. *Journal of the Arnold Arboretum* 38: 51–80, 170–198, 295–373.
<https://doi.org/10.5962/bhl.part.9105>
- Webster, G.L. (1958) A monographic study of the West Indian species of *Phyllanthus*. *Journal of the Arnold Arboretum* 39: 49–100, 111–212.
<https://doi.org/10.5962/bhl.part.19111>
- Webster, G.L. (1960) Supplement to a monographic study of the West Indian species of *Phyllanthus*. *Journal of the Arnold Arboretum* 41: 279–286.
<https://doi.org/10.5962/p.185823>
- Webster, G.L. (1966) A new species of *Phyllanthus* (Euphorbiaceae) from Central America. *Brittonia* 18: 336–342.
<https://doi.org/10.2307/2805149>
- Webster, G.L. (1967a) A remarkable new *Phyllanthus* (Euphorbiaceae) from Central America. *Annals of the Missouri Botanical Garden* 54: 194–198.
<https://doi.org/10.2307/2395014>
- Webster, G.L. (1967b) The genera of Euphorbiaceae in the southeastern United States. *Journal of the Arnold Arboretum* 48: 363–430.
<https://doi.org/10.5962/p.185727>
- Webster, G.L. (1970) A revision of *Phyllanthus* (Euphorbiaceae) in the continental United States. *Brittonia* 22: 44–76.
<https://doi.org/10.2307/2805721>
- Webster, G.L. (1978) A new Mexican species of *Phyllanthus* (Euphorbiaceae) with southern hemisphere affinities. *Rhodora* 80: 570–574.
- Webster, G.L. (1979) A revision of *Margaritaria* (Euphorbiaceae). *Journal of the Arnold Arboretum* 60: 403–444.
<https://doi.org/10.5962/bhl.part.12826>
- Webster, G.L. (1984) A revision of *Flueggea* (Euphorbiaceae). *Allertonia* 3: 259–312.
- Webster, G.L. (1986) A revision of *Phyllanthus* (Euphorbiaceae) in Eastern Melanesia. *Pacific Science* 40: 88–105.
- Webster, G.L. (1994) Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Annals of the Missouri Botanical Garden* 81: 33–144.
<https://doi.org/10.2307/2399909>
- Webster, G.L. (1995) A new species of *Phyllanthus* (Euphorbiaceae) from Ceylon. *Kew Bulletin* 50: 266.
<https://doi.org/10.2307/4110630>
- Webster, G.L. (1997) *Phyllanthus*. In: Dassanayake, M.D. & Clatyon, W.D. (Eds.) *A revised handbook to the flora of Ceylon* 11. A. Balkema, Amsterdam, pp. 206–235.
- Webster, G.L. (1999) Euphorbiaceae—*Phyllanthus*. In: Steyermark, J.A., Berry, P.E., Yatskievich, K. & Holst, B.K. (Eds.) *Flora of the Venezuelan Guayana* 5. Missouri Botanical Garden, St. Louis, pp. 191–205.
- Webster, G.L. (2001a) An unusual new species of *Phyllanthus* (Euphorbiaceae) from Colombia. *Lundellia* 4: 64–68.
<https://doi.org/10.25224/1097-993X-4.1.64>
- Webster, G.L. (2001b) Synopsis of *Croton* and *Phyllanthus* (Euphorbiaceae) in western tropical Mexico. *Contributions from the University of Michigan Herbarium* 23: 353–388.
- Webster, G.L. (2002a) A synopsis of the Brazilian taxa of *Phyllanthus* section *Phyllanthus* (Euphorbiaceae). *Lundellia* 5: 1–26.
<https://doi.org/10.25224/1097-993X-5.1.1>
- Webster, G.L. (2002b) Three new sections and a new subgenus of *Phyllanthus* (Euphorbiaceae). *Novon* 12: 290–298.
<https://doi.org/10.2307/3392970>

- Webster, G.L. (2003) A synopsis of *Phyllanthus* section *Nothoclema* (Euphorbiaceae). *Lundellia* 6: 19–36.
<https://doi.org/10.25224/1097-993X-6.1.19>
- Webster, G.L. (2004) A revision of *Phyllanthus* section *Hylaeanthus* (Euphorbiaceae). *Lundellia* 7: 11–27.
<https://doi.org/10.25224/1097-993X-7.1.11>
- Webster, G.L. (2007) Taxonomic and nomenclatural changes in American Euphorbiaceae sensu lato. *Contributions from the University of Michigan Herbarium* 25: 235–239.
- Webster, G.L. & Airy Shaw, H.K. (1971) A provisional synopsis of the New Guinea taxa of *Phyllanthus* (Euphorbiaceae). *Kew Bulletin* 26: 85–109.
<https://doi.org/10.2307/4117335>
- Webster, G.L. & Carpenter, K.J. (2002) Pollen morphology and phylogenetic relationships in neotropical *Phyllanthus* (Euphorbiaceae). *Botanical Journal of the Linnean Society* 138: 325–338.
<https://doi.org/10.1046/j.1095-8339.2002.00009.x>
- Webster, G.L. & Carpenter, K.J. (2008) Pollen morphology and systematics of palaeotropical *Phyllanthus* and related genera of subtribe Phyllanthinae (Euphorbiaceae). *Botanical Journal of the Linnean Society* 157: 591–608.
<https://doi.org/10.1111/j.1095-8339.2008.00781.x>
- Webster, G.L. & Huft, M.J. (1988) Revised synopsis of Panamanian Euphorbiaceae. *Annals of the Missouri Botanical Garden* 75: 1087–1144.
<https://doi.org/10.2307/2399381>
- Webster, G.L. & Miller, K.I. (1963) The genus *Reverchonnia* (Euphorbiaceae). *Rhodora* 65: 193–207.
- Webster, G.L. & Proctor, G.R. (1984) A new species of *Phyllanthus* (Euphorbiaceae) from the Cayman Islands. *Rhodora* 86: 121–125.
- Welwitsch, F.M.J. (1859) Apontamentos Phytogeographicos. *Annaes do Conselho Ultramarino ser. I*: 527–593.
- Wheeler, L.C. (1975) Euphorbiaceous genera lectotypified. *Taxon* 24: 534–538.
<https://doi.org/10.1002/j.1996-8175.1975.tb00345.x>
- Wight, R. (1852) *Icones plantarum Indiae Orientalis* 5. J.B. Pharoah, Madras, 354 pp.
- Wight, R. (1853) *Icones plantarum Indiae Orientalis* 6. J.B. Pharoah, Madras, 228 pp.
- Willdenow, C.L. (1805) *Species Plantarum, ed. 4*, 4 (1). Impensis G.C. Nauk, Berlin, 629 pp.
- Willdenow, C.L. (1813) *Enumeratio Plantarum Horti Regii Botanici Berolinensis*. In Taberna Libraria Scholae Realis, Berlin, 75 pp.
- Willemet, P.R.F. de P. (1796) Herbarium Mauritianum. *Annalen der Botanick* 18: 1–143.
- Wilson, P.G. (1962) *Phyllanthus petaloideus*. *Hooker's Icones Plantarum* 36: t. 3589.
- Wright, C. (1870) *Phyllanthus procerus*. In: Sauvalle, F.A., Flora Cubana. *Anales de la Academia de Ciencias Médicas, Físicas y Naturales de la Habana, Revista Científica* 7: 149.
- Wu, M.-J., Ferreras, U. & Chen, Y.-J. (2017) *Phyllanthus coi* (Phyllanthaceae), a new herbaceous species from the Philippines. *Taiwania* 62: 375–380.
- Wu, M.-J., Huang, T.-C., Liu, C.-C., Chen, Y.-J., Chang, Y.-S., Hsu, C.-L., Wu, S.-Y., Tseng, A.-Y., Chang, Y.-C., Liu, C.-C. & Kaewmuan, A. (2016) Pollen morphology and taxonomy in Malesian *Phyllanthus* (Phyllanthaceae). *The Journal of Japanese Botany* 91 (Supplement): 257–292.

Manuscripts

Available online at the website of the University of California:

http://herbarium.ucdavis.edu/webster_manuscripts.html (last accessed March 2021).

Webster G.L. (2002) Outline of the Neotropical infrageneric taxa of *Phyllanthus* (Euphorbiaceae)

<http://herbarium.ucdavis.edu/manuscripts/webster/New%20World/2002%20Outline%20neotropical%20Phyllanthus%202.pdf>

Webster G.L. (2002) Synopsis of *Phyllanthus* subgenus *Eriococcus*

<http://herbarium.ucdavis.edu/manuscripts/webster/New%20World/2002%20Synopsis%20of%20Phyllanthus%20subgenus%20Eriococcus.pdf>

Webster G.L. (2002) Synopsis of *Phyllanthus* subgenus *Kirganelia*

<http://herbarium.ucdavis.edu/manuscripts/webster/New%20World/2002%20Synopsis%20of%20Phyllanthus%20subgenus%20Kirganelia.pdf>

Webster G.L. (2002) Synopsis of *Phyllanthus* subgenus *Phyllanthus*

<http://herbarium.ucdavis.edu/manuscripts/webster/New%20World/2002%20Synopsis%20of%20Phyllanthus%20subgenus%20Phyllanthus.pdf>

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 *Paraphyllanthus* (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 grouping 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 lasiogyne 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 *Emblia 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 Radcl.-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 | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|---------------------------------|---|----------|----------|------------------|-------------|------------------|
| <i>Actephila excelsa</i> | Bouman & Yong RWB057 (HITBC) | | MN904188 | MN915296 | MN916079 | |
| <i>Antidesma bunius</i> | Gent living collection xx0Gent19002015 | | MN904189 | | MN916080 | |
| <i>Breynia amoebiflora</i> | Maxwell 90-721 (L) | | | | EU643747 | |
| <i>Breynia amoebiflora</i> | Kerr 19655 (P) | GQ503379 | GQ503437 | GQ503498 | | GQ503562 |
| <i>Breynia androgyna</i> (1) | Van Welzen 2006-4 (L) | EU623563 | GQ503439 | GQ503500 | EU643748 | GQ503564 |
| <i>Breynia androgyna</i> (3) | Kathriarachchi <i>et al.</i> 40 (K) | AY936747 | GQ503459 | GQ503517 | | GQ503588 |
| <i>Breynia asteranthos</i> | Esser 99-13 (L) | EU623565 | | GQ503501 | EU643751 | |
| <i>Breynia bicolor</i> | Esser 99-21 (L) | EU623567 | | GQ503503 | EU643754 | |
| <i>Breynia brevipes</i> | Middleton <i>et al.</i> 974 (L) | EU623568 | | | EU643755 | |
| <i>Breynia cf. macrantha</i> | Bouman & Yong RWB050 (HITBC) | MN915813 | MN904190 | MN915297 | MN916081 | MN915580 |
| <i>Breynia discigera</i> | Takeuchi <i>et al.</i> 18873 (L) | EU623550 | GQ503410 | | EU643736 | |
| <i>Breynia discocalyx</i> | Beusekom & Phengklai 566 (L) | GQ503387 | | | EU643757 | GQ503569 |
| <i>Breynia disticha</i> (1) | Bouman & Verwijns RWB024 (L) | MN915814 | MN904191 | MN915298 | MN916082 | MN915581 |
| <i>Breynia disticha</i> (2) | Yu 63 (L) | MN915815 | MN904192 | MN915299 | MN916083 | MN915582 |
| <i>Breynia fruticosa</i> | Bouman <i>et al.</i> RWB025 (L) | MN915816 | MN904193 | MN915300 | MN916084 | MN915583 |
| <i>Breynia garrettii</i> | Sino-American Guizhou Botanical Expedition 1872 (L) | EU623570 | GQ503444 | GQ503507 | EU643760 | GQ503572 |
| <i>Breynia glauca</i> | Pooma <i>et al.</i> 2702 (L) | EU623551 | GQ503411 | | EU643737 | GQ503532 |
| <i>Breynia hirsuta</i> | Larsen <i>et al.</i> 33993 (P) | GQ503391 | GQ503445 | | EU643762 | |
| <i>Breynia kerrii</i> | Van Beusekom & Phengklai 1065 (P) | EU623574 | GQ503452 | | EU643764 | GQ503579 |
| <i>Breynia lanceolata</i> | Esser 2001-4 (L) | EU623584 | | | EU643774 | |
| <i>Breynia lithophila</i> | Phonsena <i>et al.</i> 5595 (L) | | GQ503464 | GQ503522 | | GQ503595 |
| <i>Breynia macrantha</i> | Telford & Bruhl 13107 (L) | GQ503396 | | | | |
| <i>Breynia macrantha</i> | Maxwell 95-1125 (L) | | | | MT551232 | |
| <i>Breynia micrasterias</i> | Erwin & Chai S 27479 (L) | EU623578 | GQ503455 | | EU643768 | GQ503582 |
| <i>Breynia novoguineensis</i> * | Baker <i>et al.</i> 37 (L) | EU623549 | GQ503409 | GQ503472 | | GQ503530 |
| <i>Breynia oblongifolia</i> | Forster 32745 (NE) | GQ503355 | GQ503414 | GQ503475 | | GQ503534 |
| <i>Breynia orbicularis</i> | Soejarto & Southavong 10792 (L) | EU623580 | GQ503456 | GQ503513 | AY936645 | GQ503584 |
| <i>Breynia poomae</i> | Phonsena <i>et al.</i> 5245 (L) | EU623582 | GQ503457 | GQ503515 | EU643771 | GQ503586 |
| <i>Breynia repens</i> | Middleton <i>et al.</i> 2287 (L) | GQ503385 | | | | GQ503566 |
| <i>Breynia retusa</i> | Kathriarachchi <i>et al.</i> 43 (K) | | | | AY936565 | |
| <i>Breynia retusa</i> | Soejarto & Southavong 10783 (L) | GQ503358 | GQ503417 | GQ503477 | | GQ503536 |
| <i>Breynia rostrata</i> | Bouman & Yong RWB055 (HITBC) | MN915817 | MN904194 | MN915301 | MN916086 | MN915585 |
| <i>Breynia similis</i> (1) | Larsen <i>et al.</i> 46639 (L) | GQ503399 | GQ503462 | GQ503520 | EU643778 | GQ503592 |
| <i>Breynia similis</i> (2) | Bouman & Yong RWB054 (HITBC) | MN915818 | MN904195 | MN915302 | MN916085 | MN915584 |
| <i>Breynia sp.</i> (1) | Middleton 1715 (L) | MN915843 | MN904215 | MN915327 | MN916112 | MN915600 |
| <i>Breynia sp.</i> (2) | Tagane <i>et al.</i> T570 (L) | MN915844 | MN904216 | MN915328 | MN916113 | |
| <i>Breynia spatulifolia</i> | Wong s.n. (L) | EU623588 | | GQ503523 | AY936647 | GQ503596 |
| <i>Breynia stipitata</i> | Chase 14461 (K) | | | | AY552422 | |
| <i>Breynia stipitata</i> | Bruhl 2478 (NE) | GQ503359 | GQ503418 | GQ503478 | | GQ503537 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|---------------------------------------|--|----------|----------|------------------|-------------|------------------|
| <i>Breynia thorelii</i> | Van Welzen 2006-1 (L) | EU623590 | GQ503468 | GQ503526 | EU643782 | GQ503600 |
| <i>Breynia thyrsoiflora</i> | Kostermans 765 (L) | EU623591 | GQ503469 | GQ503527 | EU643783 | GQ503601 |
| <i>Breynia vestita</i> | Barker & Beaman 70 (L) | EU623553 | GQ503419 | GQ503480 | EU643738 | GQ503540 |
| <i>Breynia villosa</i> | Phengkklai <i>et al.</i> 12122 (BKF) | EU623593 | | | EU643786 | |
| <i>Breynia vitis-idea</i> (1) | Tagane <i>et al.</i> V388 (L) | MN915819 | MN904184 | MN915303 | MN916087 | |
| <i>Breynia vitis-idea</i> (2) | Tagane <i>et al.</i> V404 (L) | MN915820 | MN904185 | MN915304 | MN916088 | MN915586 |
| <i>Breynia vitis-idea</i> (3) | Majaducon 5676 (L) | MN915821 | MN904186 | MN915305 | MN916089 | |
| <i>Breynia vitis-idea</i> (4) | Yu 157 (L) | MN915822 | MN904187 | MN915306 | MN916090 | MN915587 |
| <i>Bridelia tomentosa</i> | Bouman & Yong RWB063 (HITBC) | | MN904196 | MN915307 | MN916359 | |
| <i>Cathetus aff. fasciculatus</i> (1) | Bouman & Yong RWB052 (HITBC) | MN915840 | MN904250 | MN915324 | MN916144 | MN915601 |
| <i>Cathetus aff. fasciculatus</i> (2) | Bouman & Yong RWB065 (HITBC) | MN915841 | MN904251 | MN915325 | MN916145 | MN915602 |
| <i>Cathetus aff. fasciculatus</i> (3) | Bouman & Yong RWB060 (HITBC) | MN915842 | MN904252 | MN915326 | MN916146 | MN915603 |
| <i>Cathetus beckleri</i> | Hosking 2680 (NE) | MN915861 | MN904231 | MN915347 | MN916127 | MN915618 |
| <i>Cathetus chrysanthus</i> | Munzinger & McPherson 796 (MO) | AY936680 | | | AY936585 | |
| <i>Cathetus fasciculatus</i> | Bouman <i>et al.</i> RWB026 (L) | MN915895 | MN904262 | MN915384 | MN916154 | MN915648 |
| <i>Cathetus distichus</i> | Harold st. John 17.985 (L) | MN915912 | MN904276 | MN915404 | MN916163 | MN915665 |
| <i>Cathetus exilis</i> | Hunter <i>et al.</i> 1528 (L) | MN915922 | MN904283 | | MN916362 | MN915672 |
| <i>Cathetus filicaulis</i> | Telford 13516 (NE) | MN915923 | MN904284 | MN915415 | MN916170 | MN915673 |
| <i>Cathetus gardnerianus</i> | Kathriarachchi <i>et al.</i> 42 (K) | AY936694 | MN904314 | MN915429 | AY936598 | MN915684 |
| <i>Cathetus glaucophyllus</i> (1) | Van der Brugt 1156 (WAG) | MN915938 | MN904317 | MN915432 | MN916183 | MN915687 |
| <i>Cathetus glaucophyllus</i> (2) | Haba 123 (WAG) | MN915939 | MN904318 | MN915433 | MN916340 | MN915688 |
| <i>Cathetus kerstingii</i> (1) | Darbyshire 562 (WAG) | MN915950 | MN905074 | MN915447 | MN916189 | MN915701 |
| <i>Cathetus kerstingii</i> (2) | Malaisse 14792 (WAG) | MN915951 | | MN915448 | | MN915702 |
| <i>Cathetus myrtifolius</i> (1) | Bouman & Liu RWB034 (L) | MN915995 | MN904370 | MN915495 | MN916214 | MN915736 |
| <i>Cathetus myrtifolius</i> (2) | Bouman & Yong RWB053 (HITBC) | MN915996 | MN904371 | MN915496 | MN916215 | MN915737 |
| <i>Cathetus myrtifolius</i> (3) | Yu 58 (L) | MN915997 | MN904372 | | MN916216 | MN915738 |
| <i>Cathetus patentipilis</i> * | Bruhl 1810 (NE) | MN916020 | MN904392 | MN915518 | MN916234 | MN915759 |
| <i>Cathetus petraeus</i> | Blyden 1037 (WAG) | MN916026 | MN904397 | MN915524 | MN916239 | MN915763 |
| <i>Cathetus recurvatus</i> | Wilson 612 (NE) | MN916046 | MN904414 | MN915543 | MN916258 | MN915778 |
| <i>Cathetus simplex</i> (1) | Bouman RWB069 (L) | MN916074 | MN904440 | MN915572 | MN916276 | MN915805 |
| <i>Cathetus simplex</i> (2) | Bouman RWB070 (L) | MN916075 | MN904441 | MN915573 | MN916277 | MN915806 |
| <i>Cathetus ussuriensis</i> | Kawakita 124 (KYO) | | FJ235366 | | FJ235274 | |
| <i>Cathetus virgatus</i> | Wrigley & Telford 46642 (K) | AY936738 | MN904442 | MN915574 | AY936639 | MN915807 |
| <i>Cathetus welwitschianus</i> | Bidgoet <i>et al.</i> 1882 (K) | AY936739 | | | AY936640 | |
| <i>Cathetus wheeleri</i> | Kathriarachchi <i>et al.</i> 33 (K) | AY936740 | MN904445 | MN915577 | AY936641 | MN915810 |
| <i>Cicca ambatovolanus</i> | Randriamampionona <i>et al.</i> 51 (K) | MN915848 | MN904218 | MN915332 | MN916115 | MN915605 |
| <i>Cicca ankarana</i> | Ralimanana <i>et al.</i> 663 (K) | MN915851 | MN904221 | MN915335 | MN916118 | MN915608 |
| <i>Cicca ankaratrae</i> | Rakotonasolo & Zachary 802 (K) | MN915852 | MN904222 | MN915336 | MN916119 | MN915609 |
| <i>Cicca bernieranus</i> | Phillipson 5373 (K) | MN915862 | MN904232 | MN915348 | MN916128 | MN915619 |
| <i>Cicca betsileanus</i> | Labat 2402 (K) | MN915863 | MN904233 | MN915349 | MN916360 | MN915620 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | accD-psal | matK | trnS-trnG |
|---|-------------------------------------|------------|-------------|------------------|-------------|------------------|
| <i>Cicca chacoensis</i> | Krapovickas <i>et al.</i> 45628 (K) | AY936677 | | | AY936582 | |
| <i>Cicca cryptophila</i> | Dumetz 593 (WAG) | MN915899 | MN904265 | MN915390 | MN916358 | MN915653 |
| <i>Cicca delpyana</i> (1) | Kami 1215 (WAG) | MN915906 | | MN915397 | MN916161 | MN915659 |
| <i>Cicca delpyana</i> (2) | M'Boungou 659 (WAG) | | MN904272 | MN915398 | MN916160 | |
| <i>Cicca elisiae</i> | Davidse & Gonzalez 13359 (L) | MN915916 | MN904278 | MN915408 | MN916337 | MN915667 |
| <i>Cicca engleri</i> | Mwangulango 1138 (WAG) | | MN905066 | MN915410 | MN916168 | MN915669 |
| <i>Cicca humbertii</i> | Kawakita 235 (KYO) | | FJ235345 | | FJ235253 | |
| <i>Cicca kidna</i> | Cheek 11531 | FR715993 | | | FR715992 | |
| <i>Cicca lichenisilvae</i> | Antilahimena 7638 (MO) | | MN904343 | MN915464 | MN916199 | |
| <i>Cicca mantadiensis</i> (1) | Rasoazanany 110 (MO) | MN915979 | MN904353 | MN915479 | MN916204 | |
| <i>Cicca mantadiensis</i> (2) | Rasoazanany 514 (MO) | MN915980 | MN904354 | MN915480 | MN916319 | |
| <i>Cicca marojejiensis</i> | Kawakita 243 (KYO) | | FJ235346 | | FJ235254 | |
| <i>Cicca oreichitius</i> | Antilahimena 4824 (MO) | MN916013 | MN904385 | | MN916226 | |
| <i>Cicca perrieri</i> | Rakotonasolo <i>et al.</i> 814 (K) | MN916024 | MN904395 | MN915522 | MN916238 | MN915762 |
| <i>Cicca philippioides</i> | Ralimanana <i>et al.</i> 627 (K) | MN916027 | MN904398 | MN915525 | MN916240 | MN915764 |
| <i>Cicca physocarpa</i> | McPherson 16148 (WAG) | MN916030 | MN904401 | MN915528 | MN916243 | MN915766 |
| <i>Cicca pinnata</i> | Mav 1580 (K) | MN916032 | MN904403 | MN915530 | MN916245 | MN915704 |
| <i>Cicca polyantha</i> | Breteler 1938 (WAG) | MN916033 | | MN915531 | MN916246 | MN915767 |
| <i>Cicca sambiranensis</i> | Bürki <i>et al.</i> 3 (K) | MN916053 | MN904421 | MN915552 | MN916315 | MN915784 |
| <i>Cicca sp.</i> | Ravelonarivo 3808 (MO) | MN915845 | MN904295 | MN915329 | MN916282 | |
| <i>Moeroris vakinankaratrae</i> | Ralimanana <i>et al.</i> 435 (K) | AY936737 | | | AY936638 | |
| <i>Dendrophyllanthus aff. Comptonii</i> | Munzinger 608 (MO) | MN915839 | MN904214 | MN915323 | MN916111 | |
| <i>Dendrophyllanthus bourgeoisii</i> | McMillan 5201 (WAG) | MN915870 | MN905064 | MN915357 | MN916134 | |
| <i>Dendrophyllanthus bupleuroides</i> | Mcpherson 18692 (MO) | MN915872 | MN904237 | MN915359 | MN916136 | |
| <i>Dendrophyllanthus castus</i> (1) | Mackee 16581 (L) | MN915879 | MN904246 | MN915367 | MN916327 | MN915632 |
| <i>Dendrophyllanthus castus</i> (2) | Mcpherson 19255 (MO) | MN915880 | MN904245 | MN915368 | MN916304 | |
| <i>Dendrophyllanthus caudatus</i> | Kawakita 278 (KYO) | | FJ235351 | | FJ235259 | |
| <i>Dendrophyllanthus chamaecerasus</i> | Munzinger & McPherson 573 (MO) | AY936678 | | | AY936583 | |
| <i>Dendrophyllanthus clamboides</i> | Forster 26376 (L) | MN915893 | MN904260 | MN915382 | MN916152 | MN915646 |
| <i>Dendrophyllanthus cuscutiflorus</i> | Yu 61 (L) | MN915901 | MN904268 | MN915392 | MN916299 | MN915654 |
| <i>Dendrophyllanthus dallachyanus</i> | Forster 32938 (NE) | | | MN915393 | MN916298 | MN915655 |
| <i>Dendrophyllanthus dzumacensis</i> | Jaffre 2412 (L) | MN915913 | MN905065 | MN915405 | MN916164 | MN915666 |
| <i>Dendrophyllanthus erwinii</i> | Mitchell PRP1456 (NE) | MN915920 | MN904281 | MN915413 | MN916338 | |
| <i>Dendrophyllanthus favieri</i> | McPherson & Munzinger 18028 (MO) | AY936690 | | | AY936596 | |
| <i>Dendrophyllanthus finschii</i> | Takeuchi & Ama 15603 (L) | MN915924 | MN904285 | MN915416 | MN916171 | MN915674 |
| <i>Dendrophyllanthus guillauminii</i> | Kawakita 273 (KYO) | | FJ235353 | | FJ235261 | |
| <i>Dendrophyllanthus hypospodius</i> | Bruhl <i>et al.</i> 1123 (L) | | GQ503435 | GQ503495 | EU643744 | GQ503559 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | accD-psal | matK | trnS-trnG |
|---|---|------------|-------------|------------------|-------------|------------------|
| <i>Dendrophyllanthus kanalensis</i> | McPherson & Van der Werff 17886 (K) | AY936701 | | | AY936604 | |
| <i>Dendrophyllanthus koniamboensis</i> | Kawakita 277 (KYO) | | FJ235350 | | FJ235258 | |
| <i>Dendrophyllanthus koumacensis</i> | McPherson 19163A (MO) | MN915953 | MN904331 | MN915451 | MN916191 | |
| <i>Dendrophyllanthus lacunarius</i> | Bates 62700 (NE) | MN915955 | MN904333 | MN915453 | MN916312 | MN915706 |
| <i>Dendrophyllanthus lacunellus</i> | Bates 62500 (NE) | MN915956 | MN904334 | MN915454 | MN916313 | MN915707 |
| <i>Dendrophyllanthus ligustrifolius</i> (1) | McPherson 19091 (MO) | MN915965 | MN904344 | MN915465 | MN916310 | |
| <i>Dendrophyllanthus ligustrifolius</i> (2) | McPherson 5025 (L) | MN915966 | MN904309 | MN915466 | MN916311 | MN915714 |
| <i>Dendrophyllanthus loranthoides</i> | MacKee 31810 (K) | AY936705 | | | AY936607 | |
| <i>Dendrophyllanthus mangelotii</i> | Kawakita 270 (KYO) | | FJ235349 | | FJ235257 | |
| <i>Dendrophyllanthus pancherianus</i> | McPherson & Munzinger 18264 (K) | AY936721 | MN904391 | MN915517 | AY936623 | MN915758 |
| <i>Dendrophyllanthus pilifer</i> | McPherson 18525 (MO) | MN916031 | MN904402 | MN915529 | MN916244 | |
| <i>Dendrophyllanthus poumensis</i> | Mackee 20748 (L) | MN916039 | MN904408 | MN915537 | MN916251 | MN915772 |
| <i>Dendrophyllanthus sauropodoides</i> | Forster 29857 (L) | EU623558 | GQ503436 | GQ503496 | EU643745 | GQ503560 |
| <i>Dendrophyllanthus serpentinus</i> | Mackee 20770 (L) | MN916057 | | MN915556 | | MN915788 |
| <i>Dendrophyllanthus tenuirhachis</i> | Yu & Tutie 165 (L) | MN916068 | MN904435 | MN915567 | MN916271 | MN915800 |
| <i>Dendrophyllanthus unifoliatus</i> | Veillon 7986 (L) | AY936734 | | | AY936635 | |
| <i>Dendrophyllanthus vulcani</i> | Kawakita 274 (KYO) | | FJ235354 | | FJ235262 | |
| <i>Emblia</i> sp. | Yu 250 (L) | MN915889 | MN904253 | MN915377 | MN916148 | MN915640 |
| <i>Emblia pachyphylla</i> (1) | Yahara <i>et al.</i> V3843 (L) | MN915853 | MN904223 | MN915337 | MN916120 | |
| <i>Emblia pachyphylla</i> (2) | Tagane <i>et al.</i> V3863 (L) | MN915854 | MN904224 | MN915338 | MN916121 | |
| <i>Emblia bokorensis</i> | Toyama <i>et al.</i> 1740 (FU) | | | MN915354 | MN916132 | |
| <i>Emblia collinsae</i> | Middleton 3302 (L) | MN915896 | MN904263 | MN915385 | MN916155 | MN915649 |
| <i>Emblia columnaris</i> (1) | Fujikawa <i>et al.</i> 095327 (L) | | MN904302 | MN915387 | MN916157 | MN915651 |
| <i>Emblia columnaris</i> (2) | Funakoshi <i>et al.</i> 085264 (L) | MN915897 | | MN915388 | MN916283 | MN915652 |
| <i>Emblia geoffrayi</i> | Larsen <i>et al.</i> 3259 (L) | MN915936 | MN904315 | MN915430 | MN935816 | MN915685 |
| <i>Emblia officinalis</i> (1) | Makino banical garden expedition(2015) 103008 | MN915917 | MN904279 | MN915409 | MN916167 | MN915668 |
| <i>Emblia officinalis</i> (2) | van Welzen 2003-11 (L) | GQ503378 | GQ503434 | GQ503494 | EU643743 | GQ503558 |
| <i>Emblia oxyphylla</i> (1) | Middleton 3191 (L) | MN916018 | MN904388 | MN915515 | MN916232 | MN915755 |
| <i>Emblia oxyphylla</i> (2) | Yu 174 (L) | MN916019 | MN904389 | | MN916233 | MN915756 |
| <i>Emblia pectinata</i> | Yu 65 (L) | MN916022 | | MN915520 | MN916236 | MN915761 |
| <i>Emblia phuquocensis</i> | Tagane <i>et al.</i> 5532 (FU) | MN916029 | MN904400 | MN915527 | MN916242 | |
| <i>Emblia racemosa</i> | Cooray 69090414 (L) | MN916035 | MN904405 | MN915533 | MN916248 | MN915769 |
| <i>Emblia rufuschaneyi</i> | Van der Ent (L) | | MN904418 | MN915547 | MN916259 | MN915781 |
| <i>Emblia saffordii</i> | Fosberg 59609 (L) | MN916050 | MN904419 | MN915549 | MN916260 | |
| <i>Emblia urinaria</i> (1) | Majaducon 5750 (L) | MN916071 | MN904437 | MN915569 | MN916273 | MN915802 |
| <i>Emblia urinaria</i> (2) | Bouman RWB018 (L) | MN916072 | MN904438 | MN915570 | MN916274 | MN915803 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|------------------------------------|---|-----------------|----------|------------------|-----------------|------------------|
| <i>Flueggea acidoton</i> | S. Fuentes et al. 868 (B, HAJB) | LS975740 | | | LS975798 | |
| <i>Flueggea virosa</i> (1) | Bouman & Yunhong RWB068 (HITBC) | MN915824 | MN904197 | MN915308 | MN916091 | |
| <i>Flueggea virosa</i> (2) | Mitchel 2890 (BRI) | MN915823 | | | MN916104 | |
| <i>Flueggea virosa</i> (3) | Chase 2104 (K) | | | | AY552426 | |
| <i>Flueggea virosa</i> (3) | Larsen et al. 45328 (L) | | GQ503420 | GQ503481 | | |
| <i>Flueggea virosa</i> (4) | Yu 64 (L) | MN915825 | MN904198 | | MN916092 | MN915588 |
| <i>Glochidion benthamianum</i> | Bruhl 1026 (NE) | GQ503363 | | GQ503482 | | GQ503541 |
| <i>Glochidion carinatum</i> | Toyama et al. 3212 (FU) | | MN904243 | MN915363 | MN916138 | |
| <i>Glochidion ellipticum</i> (1) | Bouman & Yong RWB058 (HITBC) | MN915826 | MN904199 | MN915310 | MN916093 | MN915589 |
| <i>Glochidion ellipticum</i> (2) | Bouman & Yong RWB061 (HITBC) | MN915827 | MN904200 | MN915311 | MN916094 | MN915590 |
| <i>Glochidion ellipticum</i> (3) | Bouman & Yong RWB062 (HITBC) | MN915829 | MN904202 | MN915309 | MN916096 | MN915591 |
| <i>Glochidion eriocarpum</i> | Bouman et al. RWB027 (L) | MN915828 | MN904201 | | MN916095 | MN915592 |
| <i>Glochidion ferdinandi</i> | Bruhl 2457 (NE) | GQ503366 | GQ503421 | GQ503484 | | GQ503543 |
| <i>Glochidion harveyanum</i> | Bruhl 2527 (NE) | GQ503368 | GQ503423 | GQ503486 | | GQ503545 |
| <i>Glochidion kaweesakii</i> | Pornpongrueng & Triyuttachai 1174 (KKU) | KY091120 | | | KY091108 | |
| <i>Glochidion lanceolarium</i> | Bouman & Yong RWB064 (HITBC) | MN915830 | MN904203 | MN915312 | MN916097 | MN915593 |
| <i>Glochidion lanceolatum</i> | Kawakita 116 (KYO) | AY525687 | FJ235327 | | FJ235235 | |
| <i>Glochidion lobocarpum</i> | Bruhl 1146 (NE) | GQ503371 | GQ503424 | GQ503488 | | GQ503548 |
| <i>Glochidion mirabilis</i> | Sirichamorn YSM 2009-05 (L) | HM132100 | HM132101 | HM132099 | | HM132102 |
| <i>Glochidion philippicum</i> | Forster 29379 (NE) | GQ503373 | GQ503426 | GQ503490 | | GQ503550 |
| <i>Glochidion puberum</i> | Chase 11460 (K) | AY936659 | | | AY552428 | |
| <i>Glochidion roseum</i> | Kawakita 143 (KYO) | KC913110 | FJ235332 | | FJ235240 | |
| <i>Glochidion sphaerogynum</i> (1) | Van der Scheur 128 (L) | MN915831 | MN904204 | MN915313 | MN916280 | MN915594 |
| <i>Glochidion sphaerogynum</i> (2) | Van Welzen 2003-21 (L) | EU623555 | GQ503427 | | EU643740 | GQ503551 |
| <i>Glochidion wrightii</i> | Bouman & Liu RWB032 (L) | MN915832 | MN904205 | MN915314 | MN916098 | MN915595 |
| <i>Heterosavia bahamensis</i> | Wurdack D048 (US) | AY936749 | AY830381 | | AY830284 | |
| <i>Kirganelia baccata</i> | Mitchell PRP1514 (NE) | | | MN915342 | MN916126 | MN915613 |
| <i>Kirganelia castica</i> | Wolhauser SW60172 (WAG) | MN915878 | MN904244 | MN915366 | MN916141 | |
| <i>Kirganelia ciccoides</i> | Paijmans 2876 (DAV) | MN915891 | | | MN916150 | |
| <i>Kirganelia dinklagei</i> (1) | Bissiengou (WAG) | MN915908 | MN904273 | MN915399 | MN916333 | MN915660 |
| <i>Kirganelia dinklagei</i> (2) | Maas 9993 (WAG) | MN915909 | MN904274 | MN915400 | MN916334 | MN915661 |
| <i>Kirganelia flexuosa</i> (1) | Chow 132 (L) | MN915927 | MN904289 | MN915419 | MN916173 | MN915677 |
| <i>Kirganelia flexuosa</i> (2) | Mcnamara 162 Living collection Berkeley | MN915928 | MN904290 | MN915420 | MN916174 | MN915678 |
| <i>Kirganelia flexuosa</i> (3) | Aung et al. 092433 (MBK) | MN915929 | MN904288 | MN915421 | MN916172 | MN915679 |
| <i>Kirganelia fuscolorida</i> (1) | Dorr 3650 (WAG) | MN915933 | MN905068 | MN915425 | MN916180 | |
| <i>Kirganelia fuscolorida</i> (2) | Schatz 1737 (WAG) | MN915934 | MN904296 | MN915426 | MN916179 | |
| <i>Kirganelia glauca</i> | Bouman & Liu RWB028 (L) | MN915940 | MN904291 | MN915434 | MN916175 | MN915689 |
| <i>Kirganelia matitanensis</i> | Ravelonarivo 4276 (MO) | MN915981 | MN904355 | MN915481 | MN916205 | |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|------------------------------------|--|----------|----------|------------------|-------------|------------------|
| <i>Kirganelia microcarpa</i> (1) | Bouman & Yong RWB056 (HITBC) | MN915985 | MN904358 | MN915483 | MN916207 | MN915729 |
| <i>Kirganelia microcarpa</i> (2) | Yang <i>et al.</i> V2332 (L) | MN915986 | MN904359 | MN915484 | MN916356 | |
| <i>Kirganelia microcarpa</i> (3) | Tanaka <i>et al.</i> MY112 (L) | MN915987 | MN904360 | MN915485 | MN916346 | |
| <i>Kirganelia microcarpa</i> (4) | Yahara <i>et al.</i> 4346 (L) | | MN904361 | MN915486 | MN916208 | |
| <i>Kirganelia muelleriana</i> (1) | Kew Seed bank collection 145024 | MN915991 | MN904366 | MN915491 | MN916295 | |
| <i>Kirganelia muelleriana</i> (2) | Bingham 6893 (WAG) | MN915992 | MN904368 | MN915492 | MN916212 | MN915734 |
| <i>Kirganelia muelleriana</i> (3) | Jongkind 39824 (WAG) | MN915993 | MN904367 | MN915493 | MN916211 | MN915735 |
| <i>Kirganelia muelleriana</i> (4) | Wieringa 7074 (WAG) | MN915994 | MN904369 | MN915494 | MN916213 | |
| <i>Kirganelia novae-hollandiae</i> | Telford 13024 (NE) | MN916001 | MN904376 | MN915500 | MN916219 | MN915741 |
| <i>Kirganelia oligosperma</i> | Kawakita 101 (KYO) | | FJ235360 | | FJ235268 | |
| <i>Kirganelia ovalifolia</i> (1) | Mallaisse 12688 (WAG) | MN916014 | MN904312 | MN915512 | MN916227 | MN915751 |
| <i>Kirganelia ovalifolia</i> (2) | de Wilde 7622 (WAG) | MN916015 | | MN915513 | MN916228 | MN915752 |
| <i>Kirganelia ovalifolia</i> (3) | Friis 13337 (WAG) | MN916016 | MN904301 | MN915514 | MN916229 | MN915753 |
| <i>Kirganelia pervilleana</i> (1) | Hoffmann <i>et al.</i> 392 (K) | AY936723 | | | AY936625 | |
| <i>Kirganelia pervilleana</i> (2) | Randrianasolo 526 (MO) | MN916025 | MN904396 | MN915523 | MN916351 | |
| <i>Kirganelia polypserma</i> (1) | Kew seed bank HBL20160135 (Kew seed bank 174282) | MN916037 | MN904406 | MN915535 | MN916249 | |
| <i>Kirganelia polypserma</i> (2) | Saolomao 40 (WAG) | MN916038 | MN904407 | MN915536 | MN916250 | MN915770 |
| <i>Kirganelia polypserma</i> (3) | Friis 10341 (WAG) | MN916036 | MN904386 | MN915534 | MN916230 | MN915771 |
| <i>Kirganelia purpurea</i> | Ward <i>et al.</i> 10442 (K) | MN916042 | MN904411 | MN915540 | MN916254 | MN915775 |
| <i>Leptopus chinensis</i> | Brownless (L) | MN915833 | MN904206 | MN915315 | MN916099 | |
| <i>Lingelsheimia sp.</i> | Rabenantoandro <i>et al.</i> 1115 (MO) | AY936662 | AY830375 | | AY830272 | |
| <i>Lysiandra calycina</i> | Chase MWC 2163 (K) | AY936674 | AY579869 | | AY552446 | |
| <i>Lysiandra carpentariae</i> | Clarkson & Neldner 8410 (L) | MN915877 | MN905063 | MN915365 | MN916140 | MN915631 |
| <i>Lysiandra cauticola</i> | Mitchell 837 (NE) | MN915881 | MN904247 | MN915369 | MN916303 | MN915633 |
| <i>Lysiandra cf. carpentariae</i> | Hyland 8033 (L) | MN915888 | MN904256 | MN915376 | MN916147 | MN915639 |
| <i>Lysiandra collina</i> | Telford & Bruhl 13119 (L) | | MN904264 | MN915386 | MN916156 | MN915650 |
| <i>Lysiandra flagellaris</i> | Fryxell & Craven (L) | MN915926 | MN904287 | MN915418 | MN916307 | MN915676 |
| <i>Lysiandra fuernrohrii</i> | Coveny 13478 (NE) | | MN904294 | | MN916178 | |
| <i>Lysiandra grandisepala</i> | Albrecht 13268 (NE) | MN915942 | MN904319 | MN915436 | MN916289 | MN915690 |
| <i>Lysiandra graniticola</i> * | Telford 13004 (NE) | MN915943 | MN904320 | MN915437 | MN916185 | MN915691 |
| <i>Lysiandra gunnii</i> | Coveny 11474 (L) | MN915944 | MN904322 | MN915439 | MN916290 | MN915693 |
| <i>Lysiandra hebecarpa</i> | Copeland NE66669 (NE) | | MN904324 | | MN916308 | MN915695 |
| <i>Lysiandra hirtella</i> | Pedersen 1328 (L) | MN915947 | MN904326 | MN915442 | MN916187 | MN915697 |
| <i>Lysiandra microclada</i> | Telford 13038 (L) | MN915988 | MN904362 | MN915487 | MN916320 | MN915730 |
| <i>Lysiandra mitchellii</i> | Bruhl 1919B (NE) | MN915990 | MN904365 | MN915490 | MN916210 | MN915733 |
| <i>Lysiandra subcrenulata</i> | Streimann s.n. (L) | MN916063 | MN904432 | | MN916270 | MN915795 |
| <i>Lysiandra trachygyne</i> | Egan 2886 (NE) | MN916069 | MN904436 | MN915568 | MN916294 | MN915801 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|------------------------------------|---|-----------------|----------|------------------|-----------------|------------------|
| <i>Margaritaria anomala</i> | Ramison 413 (MO) | MN915834 | | | MN916100 | |
| <i>Margaritaria discoidea</i> (1) | Nicholson 1 (L) | | MN904208 | MN915317 | MN916102 | |
| <i>Margaritaria discoidea</i> (2) | Nicholson s.n. (L) | | MN904207 | MN915316 | MN916101 | |
| <i>Margaritaria dubiumtraceyi</i> | Forster 29387 (BRI) | | | MN935815 | MN916103 | |
| <i>Margaritaria indica</i> | Orr 80532 | | MN904209 | MN915318 | MN916105 | |
| <i>Margaritaria nobilis</i> | Orr 875422 | | MN904210 | MN915319 | MN916106 | MN915596 |
| <i>Margaritaria rhomboidalis</i> | Rabenantoandro <i>et al.</i> 656 (K) | AY936665 | | | AY936571 | |
| <i>Margaritaria sp. Uganda</i> | Nicholson 3a (L) | MN915835 | MN904211 | MN915320 | MN916107 | MN915597 |
| <i>Moeroris sp.</i> | Ravelonarivo 4264 (MO) | MN915846 | | MN915330 | MN916281 | |
| <i>Moeroris amara</i> (1) | van Welzen 2006-5(L) | EU623557 | GQ503433 | GQ503493 | EU643742 | GQ503557 |
| <i>Moeroris amara</i> (2) | Wieringa 8189 (WAG) | MN915847 | MN904217 | MN915331 | MN916114 | |
| <i>Moeroris arenaria</i> | Worthington 18323 (L) | AY936743 | AY830380 | | AY830280 | |
| <i>Moeroris boehmii</i> (1) | Gereau 5007 (WAG) | MN915864 | MN904254 | MN915350 | MN916302 | MN915621 |
| <i>Moeroris boehmii</i> (2) | Wieringa 8841 (WAG) | MN915865 | MN904234 | MN915351 | MN916129 | MN915622 |
| <i>Moeroris boehmii</i> (3) | Bidgood 6838 (WAG) | MN915866 | MN904235 | MN915352 | MN916130 | MN915623 |
| <i>Moeroris boehmii</i> (4) | Lisowski 13765 (WAG) | MN915867 | MN904303 | MN915353 | MN916131 | MN915624 |
| <i>Moeroris bongensis</i> * | de Wilde 7858 (WAG) | MN915868 | MN904305 | MN915355 | MN916284 | |
| <i>Moeroris caesiifolia</i> | Cheek 10376 (WAG) | MN915875 | MN904242 | MN915362 | MN916137 | MN915629 |
| <i>Moeroris ceratostemon</i> | Bidgood 6776 (WAG) | MN915882 | MN904248 | MN915370 | MN916142 | MN915634 |
| <i>Moeroris cf. boehmii</i> | Friis 13159 (WAG) | MN915883 | MN904249 | MN915371 | MN916143 | MN915635 |
| <i>Moeroris cf. fischeri</i> | de Wilde 4391 (WAG) | MN915887 | MN905067 | MN915375 | MN916343 | MN915725 |
| <i>Moeroris cf. rotundifolia</i> | Nicholson 2 (L) | | MN904329 | MN915446 | MN916342 | MN915700 |
| <i>Moeroris coursii</i> | Razafindrahaja 184 (MO) | MN915898 | MN904266 | MN915389 | MN916329 | |
| <i>Moeroris debilis</i> (1) | Bouman & Liu RWB037 (L) | MN915903 | MN904269 | MN915394 | MN916330 | MN915656 |
| <i>Moeroris debilis</i> (2) | Bouman RWB071 (L) | MN915904 | MN904270 | MN915395 | MN916331 | MN915657 |
| <i>Moeroris debilis</i> (3) | Kamarudim & Apok (L) | MN915905 | MN904271 | MN915396 | MN916332 | MN915658 |
| <i>Moeroris dimorpha</i> | E.R. Bcquer <i>et al.</i> HFC 87940 (HAJB) | LS975738 | | | LS975795 | |
| <i>Moeroris dinteri</i> (1) | Dinter 213 (WAG) | MN915910 | | MN915401 | MN916335 | MN915662 |
| <i>Moeroris dinteri</i> (2) | Oliver 6543 (WAG) | MN915911 | MN905069 | MN915402 | MN916336 | MN915663 |
| <i>Moeroris fischeri</i> | Gereau 1996 (WAG) | MN915925 | MN904286 | MN915417 | | MN915675 |
| <i>Moeroris fraterna</i> | Nooteboom 3010 (L) | MN915931 | | MN915423 | MN916306 | MN915681 |
| <i>Moeroris friesii</i> | Harder <i>et al.</i> 2778 (WAG) | MN915932 | MN904293 | MN915424 | MN916177 | MN915682 |
| <i>Moeroris fuertesii</i> | S. Fuentes <i>et al.</i> 294 (B, HAJB) | LS975752 | | | LS975812 | |
| <i>Moeroris gabonensis</i> (1) | Maas 10095 (WAG) | | MN904299 | MN915427 | MN916181 | MN915683 |
| <i>Moeroris gabonensis</i> (2) | Wieringa 8492 (WAG) | MN915935 | MN904313 | MN915428 | MN916182 | |
| <i>Moeroris gillettiana</i> | Germishuizen 9727 (WAG) | MN915937 | MN904316 | MN915431 | | MN915686 |
| <i>Moeroris harrisii</i> | Faulkner 3179 (WAG) | MN915945 | MN904323 | MN915440 | MN916341 | MN915694 |
| <i>Moeroris hutchinsoniana</i> (1) | Poilecot 7974 (K) | AY936697 | MN904327 | MN915443 | AY936601 | MN915698 |
| <i>Moeroris hutchinsoniana</i> (2) | Bamps 88 (WAG) | MN915948 | MN904306 | MN915444 | | |
| <i>Moeroris kaessneri</i> | Pocs 89182 (K) | AY936700 | | | AY936603 | |
| <i>Moeroris leucantha</i> (1) | de Wilde 4604 (WAG) | MN915962 | MN904300 | MN915460 | MN916149 | MN915642 |
| <i>Moeroris leucantha</i> (2) | Friis 8619 (WAG) | MN915963 | MN904340 | MN915461 | MN916344 | MN915713 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|-------------------------------------|---|-----------------|----------|------------------|-----------------|------------------|
| <i>Moeroris leucocalyx</i> (1) | Bidgood 7161 (WAG) | | MN904341 | MN915462 | MN916197 | |
| <i>Moeroris leucocalyx</i> (2) | Bidgood 6969 (WAG) | MN915964 | MN904342 | MN915463 | MN916198 | |
| <i>Moeroris limmuensis</i> | de Wilde 6524 (WAG) | MN915967 | MN904345 | MN915467 | MN916291 | MN915715 |
| <i>Moeroris loandensis</i> (1) | Pawek R597 (WAG) | MN915968 | MN904346 | MN915469 | MN916201 | MN915717 |
| <i>Moeroris loandensis</i> (2) | Pawek 12535 (WAG) | MN915970 | MN904297 | MN915470 | MN916202 | MN915718 |
| <i>Moeroris loandensis</i> (3) | Nuvunga 526 (WAG) | MN915969 | MN905072 | MN915471 | MN916203 | MN915719 |
| <i>Moeroris lokohensis</i> | Antilahimena 8041 (MO) | MN915971 | MN904347 | | MN916316 | |
| <i>Moeroris macrantha</i> | Biegel <i>et al.</i> 4847 (WAG) | MN915972 | MN905075 | MN915472 | MN916292 | MN915720 |
| <i>Moeroris madagascariensis</i> | McPherson 18925 (MO) | MN915973 | MN904348 | MN915473 | MN916317 | |
| <i>Moeroris maderaspatensis</i> | Hunter <i>et al.</i> 1532 (K) | AY936707 | | | AY936609 | |
| <i>Moeroris magnificens</i> | van der Burgt 1196 (WAG) | MN915975 | MN904349 | MN915475 | MN916345 | MN915722 |
| <i>Moeroris manniana</i> (1) | Raynal 12256 (WAG) | MN915977 | MN904351 | MN915477 | MN916347 | MN915724 |
| <i>Moeroris manniana</i> (2) | Biye 129 (WAG) | MN915978 | MN904352 | MN915478 | | MN915726 |
| <i>Moeroris melleri</i> | Lowry <i>et al.</i> 5814 (K) | MN915983 | MN904357 | MN915482 | MN916314 | MN915728 |
| <i>Moeroris nirurioides</i> (1) | Bidgood 8049 (WAG) | MN915998 | MN904374 | MN915497 | MN916305 | MN915739 |
| <i>Moeroris nirurioides</i> (2) | Wieringa 7502 (WAG) | MN915999 | MN904375 | MN915498 | MN916218 | MN915740 |
| <i>Moeroris nummulariifolia</i> (1) | Nicholson 3b (L) | MN916002 | MN904377 | MN915501 | MN916288 | MN915742 |
| <i>Moeroris nummulariifolia</i> (2) | Wieringa 8374 (WAG) | MN916003 | MN904380 | MN915502 | MN916361 | MN915744 |
| <i>Moeroris nummulariifolia</i> (3) | van Andel 5732 (WAG) | MN916004 | MN904381 | MN915503 | MN916223 | MN915743 |
| <i>Moeroris nummulariifolia</i> (4) | Mwangoka 5900 (WAG) | MN916005 | MN904379 | MN915504 | MN916222 | |
| <i>Moeroris nummulariifolia</i> (5) | Razafitsalama 235 (MO) | MN916006 | MN904378 | MN915505 | MN916220 | |
| <i>Moeroris nummulariifolia</i> (6) | Blaxell 1118 (U) | MN916007 | MN904310 | MN915506 | MN916221 | MN915745 |
| <i>Moeroris nyale</i> | Etuge 4453 (WAG) | MN916008 | MN904382 | MN915507 | MN916224 | MN915746 |
| <i>Moeroris odontadenia</i> (1) | Darbyshire 207 (WAG) | MN916009 | MN904311 | MN915508 | MN916348 | MN915747 |
| <i>Moeroris odontadenia</i> (2) | Bouman & Verwijs RWB025 (L) | MN916010 | MN904383 | MN915509 | MN916349 | MN915748 |
| <i>Moeroris odontadenia</i> (3) | Wieringa 7665 (WAG) | MN916011 | MN904384 | MN915510 | MN916350 | MN915749 |
| <i>Moeroris oxycoccifolia</i> | Gereau 5219 (WAG) | MN916017 | MN904387 | | MN916231 | MN915754 |
| <i>Moeroris paxii</i> | Bidgood 2983 (WAG) | MN916021 | MN904393 | MN915519 | MN916235 | MN915760 |
| <i>Moeroris pentandra</i> | Kew Seed bank collection 519962 | MN916023 | MN904394 | MN915521 | MN916237 | |
| <i>Moeroris phillyreifolia</i> | van Nek 2188 (WAG) | MN916028 | MN904399 | MN915526 | MN916241 | MN915765 |
| <i>Moeroris procera</i> (1) | S. Fuentes <i>et al.</i> 428 (B, HAJB) | LS975737 | | | LS975794 | |
| <i>Moeroris procera</i> (2) | S. Fuentes <i>et al.</i> 414 (B, HAJB) | LS975769 | | | LS975830 | |
| <i>Moeroris rangoloakensis</i> | Schatz <i>et al.</i> 3709 (K) | MN916045 | MN904413 | MN915542 | MN916257 | MN915777 |
| <i>Moeroris rheedii</i> | Kathriarachchi <i>et al.</i> 1 (K) | AY936729 | MN904415 | MN915544 | AY936630 | MN915779 |
| <i>Moeroris rotundifolia</i> | Wieringa 8849 (WAG) | MN916047 | MN904416 | MN915545 | MN916352 | MN915780 |
| <i>Moeroris sepialis</i> | Luke 7112 (K) | AY936732 | | | AY936633 | |
| <i>Moeroris stipulata</i> (1) | Jansen-Jacobs 2813 (U) | | MN904430 | MN915561 | MN916268 | MN915793 |
| <i>Moeroris stipulata</i> (2) | Gieteling 114 (WAG) | MN916062 | MN904431 | MN915562 | MN916269 | MN915794 |
| <i>Moeroris tenella</i> (1) | Bruhl 2633 (L) | MN916065 | MN904433 | MN915564 | MN916354 | MN915797 |
| <i>Moeroris tenella</i> (2) | Bouman RWB019 (L) | MN916066 | MN904434 | MN915565 | MN916355 | MN915798 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|---|---|----------|----------|------------------|-------------|------------------|
| <i>Moeroris tenella</i> (3) | Groenendijk 15 (WAG) | MN916067 | MN904308 | MN915566 | MN916357 | MN915799 |
| <i>Moeroris wakensis</i> * | Wieringa 5107 (WAG) | | MN904443 | MN915575 | | MN915808 |
| <i>Nellica magudensis</i> | Blokhuis 50 (WAG) | MN915976 | MN904350 | MN915476 | MN916318 | MN915723 |
| <i>Nellica mendoncae</i> | de Wilde 6464 (WAG) | MN915984 | | | | |
| <i>Nellica polygonoides</i> | Kim & Miller 1078 (U) | MN916034 | MN904404 | MN915532 | MN916247 | MN915768 |
| <i>Notoleptopus decaisnei</i> | Evans 3222 (K) | AM745836 | | | AM745833 | |
| <i>Notoleptopus decaisnei</i> | Fraser 267 (L) | | GQ503431 | GQ503491 | | GQ503555 |
| <i>Nymphanthus balgooyi</i> (1) | Van der Ent | MN915857 | MN904227 | MN915343 | MN916300 | MN915614 |
| <i>Nymphanthus balgooyi</i> (2) | Yu 192 (L) | MN915858 | MN904228 | MN915344 | MN916301 | MN915615 |
| <i>Nymphanthus balgooyi</i> (3) | Yu 259 (L) | MN915859 | MN904229 | MN915345 | MN916324 | MN915616 |
| <i>Nymphanthus balgooyi</i> (4) | Agoo 5700 (L) | MN915860 | MN904230 | MN915346 | MN916325 | MN915617 |
| <i>Nymphanthus buxifolius</i> (1) | Yu 163 (L) | MN915873 | MN904240 | MN915360 | MN916326 | MN915627 |
| <i>Nymphanthus buxifolius</i> (2) | Yu 167 (L) | MN915874 | MN904241 | MN915361 | MN916285 | MN915628 |
| <i>Nymphanthus cf.</i> <i>buxifolius</i> (1) | Agoo 5659 (L) | MN915884 | MN904238 | MN915372 | MN916286 | MN915636 |
| <i>Nymphanthus cf.</i> <i>buxifolius</i> (2) | Agoo 5683 (L) | MN915885 | MN905070 | MN915373 | MN916287 | MN915637 |
| <i>Nymphanthus cf.</i> <i>buxifolius</i> (3) | Agoo 5738 (L) | MN915886 | MN904239 | MN915374 | MN916328 | MN915638 |
| <i>Nymphanthus cf.</i> <i>sootepensis</i> | Bouman & Yong RWB059 (HITBC) | MN915890 | MN904428 | MN915378 | MN916267 | MN915643 |
| <i>Nymphanthus curranii</i> | Yu 261 (L) | MN915900 | MN904267 | MN915391 | MN916158 | MN915604 |
| <i>Nymphanthus elegans</i> (1) | Yahara <i>et al.</i> V3499 (L) | MN915914 | | MN915406 | MN916165 | |
| <i>Nymphanthus elegans</i> (2) | Yahara <i>et al.</i> V5597 (L) | MN915915 | MN904277 | MN915407 | MN916166 | |
| <i>Nymphanthus floribundus</i> | Kathriarachchi <i>et al.</i> 66 (K) | AY936682 | MN904259 | MN915381 | AY936587 | |
| <i>Nymphanthus glaucescens</i> (1) | Bouman & Yong RWB066 (HITBC) | MN916040 | MN904409 | MN915538 | MN916252 | MN915773 |
| <i>Nymphanthus glaucescens</i> (2) | Esser 98-68 (L) | MN916041 | MN904410 | MN915539 | MN916253 | MN915774 |
| <i>Nymphanthus gomphocarpus</i> | Klackenberg & Lundin 579 (L) | MN915941 | MN905073 | MN915435 | MN916184 | |
| <i>Nymphanthus kinabalucius</i> | Van der Ent (Kinabalu Parcs living collection) | MN915952 | MN904330 | MN915449 | MN916190 | MN915703 |
| <i>Nymphanthus laciniatus</i> | Agoo 5660 (L) | MN915954 | MN904332 | MN915452 | MN916192 | MN915705 |
| <i>Nymphanthus leptocladus</i> | Bouman & Yong RWB051 (HITBC) | MN915961 | MN904339 | MN915459 | MN916196 | MN915712 |
| <i>Nymphanthus longifolius</i> | TRP-5004102 (BK) | AB550090 | | | | |
| <i>Nymphanthus megalanthus</i> | Calaramo (L) | MN915982 | MN904356 | | MN916206 | MN915727 |
| <i>Nymphanthus ruber</i> | Lee <i>et al.</i> s.n. (CUHK) | AY765298 | | | | |
| <i>Nymphanthus rubescens</i> | Yahara <i>et al.</i> V2902 (L) | MN916048 | MN904417 | MN915546 | MN916322 | |
| <i>Nymphanthus sootepensis</i> (1) | Makino banical garden expedition(2015) 103251 | MN916059 | MN904426 | MN915558 | MN916297 | MN915790 |
| <i>Nymphanthus sootepensis</i> (2) | Makino banical garden expedition(2015) 103753 | MN916060 | MN904427 | MN915559 | MN916266 | MN915791 |
| <i>Nymphanthus tetrandrus</i> | Fujikawa <i>et al.</i> 053175 (L) | MN916058 | MN904425 | MN915557 | MN916296 | MN915789 |
| <i>Nymphanthus watsonii</i> | Yu 225 (L) | MN916076 | MN904444 | MN915576 | MN916278 | MN915809 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|---------------------------------------|---|-----------------|----------|------------------|-----------------|------------------|
| <i>Phyllanthus acidus</i> | van welzen 2003-14(L) | MN915836 | GQ503432 | GQ503492 | MN916108 | GQ503556 |
| <i>Phyllanthus acuminatus</i> (1) | Breteler 4238 (WAG) | MN915837 | MN904212 | MN915321 | MN916109 | MN915598 |
| <i>Phyllanthus acuminatus</i> (2) | Wallnöfer 6031 (U) | MN915838 | MN904213 | MN915322 | MN916110 | MN915599 |
| <i>Phyllanthus aeneus</i> | Kawakita 272 (KYO) | | FJ235352 | | FJ235260 | |
| <i>Phyllanthus angustifolius</i> | Lauerer 091479 | MN915849 | MN904219 | MN915333 | MN916116 | MN915606 |
| <i>Phyllanthus anisobolus</i> | Liesner 14363 (U) | MN915850 | MN904220 | MN915334 | MN916117 | MN915607 |
| <i>Phyllanthus arbuscula</i> | Reynders 19074182 (L) | MN915855 | MN904226 | MN915339 | MN916123 | MN915610 |
| <i>Phyllanthus arenicola</i> | Maas & Carauta (U) | | MN905071 | MN915340 | MN916124 | MN915611 |
| <i>Phyllanthus attenuatus</i> | Breteler 4696 (WAG) | MN915856 | MN904304 | MN915341 | MN916125 | MN915612 |
| <i>Phyllanthus botryanthus</i> | de Wilde 31 (WAG) | MN915869 | MN904255 | MN915356 | MN916133 | MN915625 |
| <i>Phyllanthus brasiliensis</i> | Ule 6408 (L) | MN915871 | MN904236 | MN915358 | MN916135 | MN915626 |
| <i>Phyllanthus caroliniensis</i> | Groenendijk 55 (WAG) | MN915876 | | MN915364 | MN916139 | MN915630 |
| <i>Phyllanthus cf.klotzschianus</i> | Carneiro 10 (K) | | | MN915450 | | MN915641 |
| <i>Phyllanthus chamaecristoid</i> | van Ee <i>et al.</i> 404 (K) | AY936679 | | | AY936584 | |
| <i>Phyllanthus chryseus</i> | Van Ee <i>et al.</i> 387 (K) | AY936681 | MN904257 | MN915379 | AY936586 | MN915644 |
| <i>Phyllanthus cinctus</i> | Ekman 19166 (K) | MN915892 | MN904258 | MN915380 | MN916151 | MN915645 |
| <i>Phyllanthus claussenii</i> | Hatschbach 64117 (U) | MN915894 | MN904261 | MN915383 | MN916153 | MN915647 |
| <i>Phyllanthus comosus</i> | Gutierrez <i>et al.</i> 81777 (WIS) | AY936685 | | | AY936590 | |
| <i>Phyllanthus comosus</i> (2) | T. Borsch <i>et al.</i> 4271 (B, HAJB) | LS975727 | | | LS975785 | |
| <i>Phyllanthus dawsonii</i> | da Silva 2073 (DAV) | MN915902 | | | MN916159 | |
| <i>Phyllanthus dictyospermus</i> | Santos 5712 (DAV) | MN915907 | | | MN916162 | |
| <i>Phyllanthus discolor</i> | Berazain <i>et al.</i> 71878 (K) | AY936688 | MN904275 | MN915403 | AY936593 | MN915664 |
| <i>Phyllanthus epiphyllanthus</i> (1) | Lauerer 080405 | MN915918 | MN904225 | MN915411 | MN916122 | MN915670 |
| <i>Phyllanthus epiphyllanthus</i> (2) | Reynders IPEN:XX-0-BR-19840633 (L) | MN915919 | MN904280 | MN915412 | MN916169 | MN915671 |
| <i>Phyllanthus evanescens</i> | Stevens 32461 (MO) | MN915921 | MN904282 | MN915414 | MN916339 | |
| <i>Phyllanthus excisus</i> | W. Greuter <i>et al.</i> 28281 (B, HAJB, P-Gr) | LS975746 | | | LS975806 | |
| <i>Phyllanthus fluitans</i> | Krämer xx-0-Dath-518 (L) | MN915930 | MN904292 | MN915422 | MN916176 | MN915680 |
| <i>Phyllanthus graveolens</i> | Klitgaard <i>et al.</i> 399 (K) | AY936696 | MN904321 | MN915438 | AY936600 | MN915692 |
| <i>Phyllanthus heliotropus</i> | Maas <i>et al.</i> 7762 (U) | MN915946 | MN904325 | MN915441 | MN916186 | MN915696 |
| <i>Phyllanthus incrustatus</i> | T. Borsch <i>et al.</i> 4504 (B, HAJB) | LS975731 | | | LS975788 | |
| <i>Phyllanthus juglandifolius</i> | Bouman RWB16 | MN915949 | MN904328 | MN915445 | MN916188 | MN915699 |
| <i>Phyllanthus klotzschianus</i> | Grappo <i>et al.</i> 780 (K) | AY936702 | | | AY936605 | |
| <i>Phyllanthus lamprophyllus</i> (1) | Agoo 5592 (L) | MN915957 | MN904335 | MN915455 | MN916193 | MN915708 |
| <i>Phyllanthus lamprophyllus</i> (2) | Telford & Bruhl 13049 (L) | MN915958 | MN904336 | MN915456 | MN916194 | MN915709 |
| <i>Phyllanthus lamprophyllus</i> (3) | Telford & Bruhl 13051 (L) | MN915959 | MN904337 | MN915457 | MN916195 | MN915710 |
| <i>Phyllanthus lamprophyllus</i> (4) | Yu 161 (L) | MN915960 | MN904338 | MN915458 | MN916309 | MN915711 |
| <i>Phyllanthus lindenianus</i> | S. Fuentes <i>et al.</i> 1003 (B) | LS975755 | | | LS975815 | |
| <i>Phyllanthus lindenianus</i> | Fuertes 345 (K) | | | MN915468 | MN916200 | MN915716 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psal</i> | <i>matK</i> | <i>trnS-trnG</i> |
|--|--|-----------------|----------|------------------|-----------------|------------------|
| <i>Phyllanthus madeirensis</i> | Vincentini 1206 (U) | MN915974 | MN905078 | MN915474 | MN916293 | MN915721 |
| <i>Phyllanthus maleolens</i> | S. Fuentes et al. 1121 (B) | LS975756 | | | LS975816 | |
| <i>Phyllanthus microdictyis</i> | Van Ee 399 (K) | AY936709 | MN904363 | MN915488 | AY936612 | MN915731 |
| <i>Phyllanthus mimosoides</i> | Reynders 19074179 (L) | MN915989 | MN904364 | MN915489 | MN916209 | MN915732 |
| <i>Phyllanthus mirifcus</i> | T. Borsch et al. 5021 (B, HAJB) | LS975774 | | | LS975835 | |
| <i>Phyllanthus niruri</i> | De la Quintana 333 (MO) | MN916000 | MN904373 | MN915499 | MN916217 | |
| <i>Phyllanthus nummularioides</i> | S. Fuentes et al. 880 (B) | LS975753 | | | LS975813 | |
| <i>Phyllanthus nutans</i> | S. Fuentes et al. 996 (B) | LS975754 | | | LS975814 | |
| <i>Phyllanthus orbicularis</i> | Eschevaria s.n. (L) | MN916012 | MN904298 | MN915511 | MN916225 | MN915750 |
| <i>Phyllanthus pachystylus</i> | Van Ee 402 (K) | AY936720 | MN904390 | MN915516 | AY936622 | MN915757 |
| <i>Phyllanthus phlebocarpus</i> | P.A. Gonzalez HFC 87732 (HAJB) | LS975758 | | | LS975819 | |
| <i>Phyllanthus pseudocicca</i> (1) | B. Falcon et al. HFC 87780 (HAJB) | LS975736 | | | LS975793 | |
| <i>Phyllanthus pseudocicca</i> (2) | P.A. Gonzalez HFC 87681 (HAJB) | LS975759 | | | LS975820 | |
| <i>Phyllanthus purpusii</i> | Breedlove 42730 Living collection Berkeley | MN916043 | MN904412 | MN915541 | MN916255 | MN915776 |
| <i>Phyllanthus ramillosus</i> | Arbo 6945 (DAV) | MN916044 | | | MN916256 | |
| <i>Phyllanthus ruscifolius</i> | Cuatrecasas 21631 (U) | MN916049 | MN905077 | MN915548 | | MN915782 |
| <i>Phyllanthus salviifolius</i> (1) | Balslev 1888 (U) | MN916051 | MN905076 | MN915550 | MN916261 | |
| <i>Phyllanthus salviifolius</i> (2) | Jorgensen 61204 (U) | MN916052 | MN904420 | MN915551 | MN916262 | MN915783 |
| <i>Phyllanthus sellowianus</i> (1) | Chase 14776 | MN916054 | MN904422 | MN915553 | MN916263 | MN915785 |
| <i>Phyllanthus sellowianus</i> (2) | Chase 14777 | MN916055 | MN904423 | MN915554 | MN916264 | MN915786 |
| <i>Phyllanthus sellowianus</i> (3) | Chase 14463 | MN916056 | MN904424 | MN915555 | MN916265 | MN915787 |
| <i>Phyllanthus sp. sect. Callitrichoides</i> | B. Falcon et al. HFC 87779 (HAJB) | LS975742 | | | LS975801 | |
| <i>Phyllanthus spruceanus</i> | Maas & Maas 474 (U) | MN916061 | MN904429 | MN915560 | MN916353 | MN915792 |
| <i>Phyllanthus subcarnosus</i> | T. Borsch et al. 4707 (B, HAJB) | LS975741 | | | LS975800 | |
| <i>Phyllanthus symphoricarpoides</i> | Cuatrecasas 18421 (U) | MN916064 | MN904307 | MN915563 | MN916321 | MN915796 |
| <i>Phyllanthus tuerckheinii</i> | Mendez 8022 (DAV) | MN916070 | | | MN916272 | |
| <i>Phyllanthus vacciniifolius</i> | Hokche et al. 854 (U) | MN916073 | MN904439 | MN915571 | MN916275 | MN915804 |
| <i>Phyllanthus williamioides</i> | T. Borsch et al. 4523 (B, HAJB) | LS975730 | | | LS975787 | |
| <i>Phyllanthys myrtilloides</i> subsp. <i>Alainii</i> | S. Fuentes et al. 556 (B, HAJB) | | | | LS975799 | |
| <i>Phyllanthys myrtilloides</i> subsp. <i>Erythrinus</i> | W. Greuter et al. 28014 (B, HAJB, P-Gr) | LS975734 | | | LS975791 | |
| <i>Phyllanthys myrtilloides</i> subsp. <i>Shaferi</i> | S. Fuentes et al. 426 (B, HAJB) | LS975743 | | | LS975802 | |
| <i>Phyllanthys myrtilloides</i> subsp. <i>Spathulifolius</i> | P.A. Gonzalez HFC 87731 (HAJB) | LS975772 | | | LS975833 | |
| <i>Plagiocladus diandrus</i> | Wieringa 2903 (WAG) | | | | AY936592 | |
| <i>Plagiocladus diandrus</i> | de Wilde & de Wilde 11641 (WAG) | AY936687 | | | | |
| <i>Synostemon albiflorus</i> (1) | Forster 32329 (NE) | MN916077 | MN904446 | MN915578 | MN916279 | MN915811 |

.....continued on the next page

Appendix 2. (Continued)

| Matrix name | Voucher | ITS | PHYC | <i>accD-psaI</i> | <i>matK</i> | <i>trnS-trnG</i> |
|----------------------------------|----------------------|----------|----------|------------------|-------------|------------------|
| <i>Synostemon albiflorus</i> (2) | Forster 34400 (NE) | MN916078 | MN904447 | MN915579 | MN916323 | MN915812 |
| <i>Synostemon bacciformis</i> | Cowie I 3418 (L) | GQ503382 | | GQ503502 | | |
| <i>Synostemon bacciformis</i> | Kerr 8350 (L) | | | | EU643753 | |
| <i>Synostemon bacciformis</i> | Pruesapan 2009-4 (L) | | GQ503440 | | | |
| <i>Synostemon hirtellus</i> | Bean 15558 (BRI) | EU623573 | GQ503447 | GQ503508 | EU643763 | GQ503574 |
| <i>Synostemon kakadu</i> | Bruhl 1270 (NE) | GQ503395 | GQ503451 | GQ503510 | | GQ503578 |
| <i>Synostemon sphenophyllus</i> | Gray 08597 (BRI) | GQ503402 | GQ503465 | | EU643780 | GQ503597 |
| <i>Synostemon spinosus</i> | Bean 20738 (NE) | GQ503403 | GQ503466 | GQ503524 | | GQ503598 |
| <i>Synostemon trachyspermus</i> | Bell 547 (NE) | GQ503407 | GQ503470 | GQ503528 | EU643784 | GQ503602 |

Supplementary figure 1. Phylogeny of tribe Phyllanthae 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 (*).