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

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Citation

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

Disentangling a complex genus

Systematics, biogeography and bioactivity of the genus *Phyllanthus* L. and related genera of tribe Phyllantheae (Phyllanthaceae)

Roderick Bouman

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

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Hortus botanicus Leiden & Naturalis Biodiversity Center
Leiden University
2022

Roderick W. Bouman, 2022. Disentangling a complex genus: Systematics, biogeography and bioactivity of the genus Phyllanthus L. and related genera of tribe Phyllantheae (Phyllanthaceae).
PhD thesis, University of Leiden, The Netherlands

ISBN: 978-94-6469-129-0

Front cover: *Phyllanthus emblica* L., *P. urinaria* L., *Glochidion* sp., *Breynia rostrata* Merr., *P. debilis* J.G.Klein ex Willd., *P. arbuscula* (Sw.) J.F.Gmel, *P. buxifolius* Blume, *Flueggea virosa* (Roxb. ex Willd.) Royle [*F. virosa* by R.-Y. Yu, other photos by R.W. Bouman]
Back cover: *P. buxifolius* Blume, *P. urinaria* L., *P. lamprophyllus* Müll.Arg. [Photos by R.W. Bouman]
Layout and cover design by Roderick W. Bouman
All botanical illustrations drawn by E. Winkel
Printed by ProefschriftMaken

The separate chapters may differ from the original publications. This disseration is not to be considered as effectively published in the sense of Turland NJ et al. (eds) 2018, International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code), adopted by the nineteenth International Botanical Congress Shenzhen, China, July 2017. Article 30. Regnum Vegetabile 159.

This research was carried out at Hortus botanicus Leiden, Naturalis Biodiveristy and Institute of Biology Leiden at Leiden University.

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

Proefschrift

ter verkrijging van
de graad van doctor aan de Universiteit Leiden,
op gezag van rector magnificus prof.dr.ir. H. Bijl,
volgens besluit van het college voor promoties
te verdedigen op dinsdag 6 december 2022
klokke 13:45 uur

door

Roderick Wiebe Bouman
geboren te Hilversum, Nederland
in 1991

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CHAPTER 1

General Introduction

Chapter 1

Background

Phyllanthaceae is a remarkable but understudied plant family that is classified in the Malpighiales, a difficult order often with families characterized by very small flowers, which has been the subject of several phylogenetic studies (Wurdack et al. 2004; Wurdack & Davis 2009; Xi et al. 2012). The order comprises roughly 42 families, with almost no clear apomorphies per clade and the distinctions and relations between families are still under discussion (Xi et al. 2012). One of the more difficult member families is the Euphorbiaceae, which in the past was classified in five major subfamilies: Phyllanthoideae, Oldfieldioideae, Acalyphoideae, Crotonoideae and Euphorbioideae (Webster 1994, 2014; Radcliffe-Smith 2001).

Following the results of APG II (APG 2003), Euphorbiaceae was found to be non-monophyletic and it was subsequently divided into five families: Euphorbiacaeae s.s., Phyllanthaceae and Picrodendraceae (formerly subfamily Oldfieldioideae) (APG 2003; Wurdack et al. 2009), next to the non-related Pandaceae and Putranjivaceae. The most recent molecular study by Xi et al. (2012), identified a clade as the euphorbioids, which consists of the families Euphorbiaceae, Rafflesiaceae, Peraceae, Picrodendraceae, Phyllanthaceae, Linaceae and Ixonanthaceae). While support between the major clades varies between studies (see Xi et al. 2012; Sun et al. 2016), the Picrodendraceae and Phyllanthaceae are consistently retrieved as sister groups. Picrodendraceae and Phyllanthaceae represent what is commonly known as the phyllanthoids or bi-ovulate Euphorbiaceae and these families are still sometimes treated together with Euphorbiaceae (Webster 2014). Nevertheless, the phyllanthoids are an interesting clade and particularly the family Phyllanthaceae, which contains more than 2000 species (Hoffmann et al. 2006), characterized by unisexual flowers (with a few bisexual exceptions in *Aporosa* Blume), ecarunculate seeds (except in *Glochidion* J.R.Forst. & G.Forst. and *Margaritaria* L.f.) and generally capsular fruits (Fig. 1-1).

The latest classification of Phyllanthaceae divides the family into two subfamilies and ten tribes (Fig. 1-2). A further division of Phyllanthaceae into several families seems unwarranted (but see Chakrabarty & Balakrishnan 2018). Currently 58 genera are recognised and the majority of species are found in tribe Phyllantheae. The diversity of morphological characters within this tribe has caused several issues in its taxonomy, most notably in the species rich genus *Phyllanthus* L., which was found to be paraphyletic (Wurdack et al. 2004; Samuel et al. 2005; Kathriarachchi et al. 2006). Tribe Phyllantheae was originally defined by Dumort (1829) within the Euphorbiaceae (as Phylantheae) containing the genera *Cluytia* Steud. (now Euphorbiaceae), *Xylophylla* L., *Phyllanthus*, *Kirganelia* A.Juss., *Cicca* L., *Andrachne* L. and *Bridelia* Willd. Several genera in this classification were merged with *Phyllanthus* in the second half of the 19th century (Müller 1863, 1865, 1866) and the classification

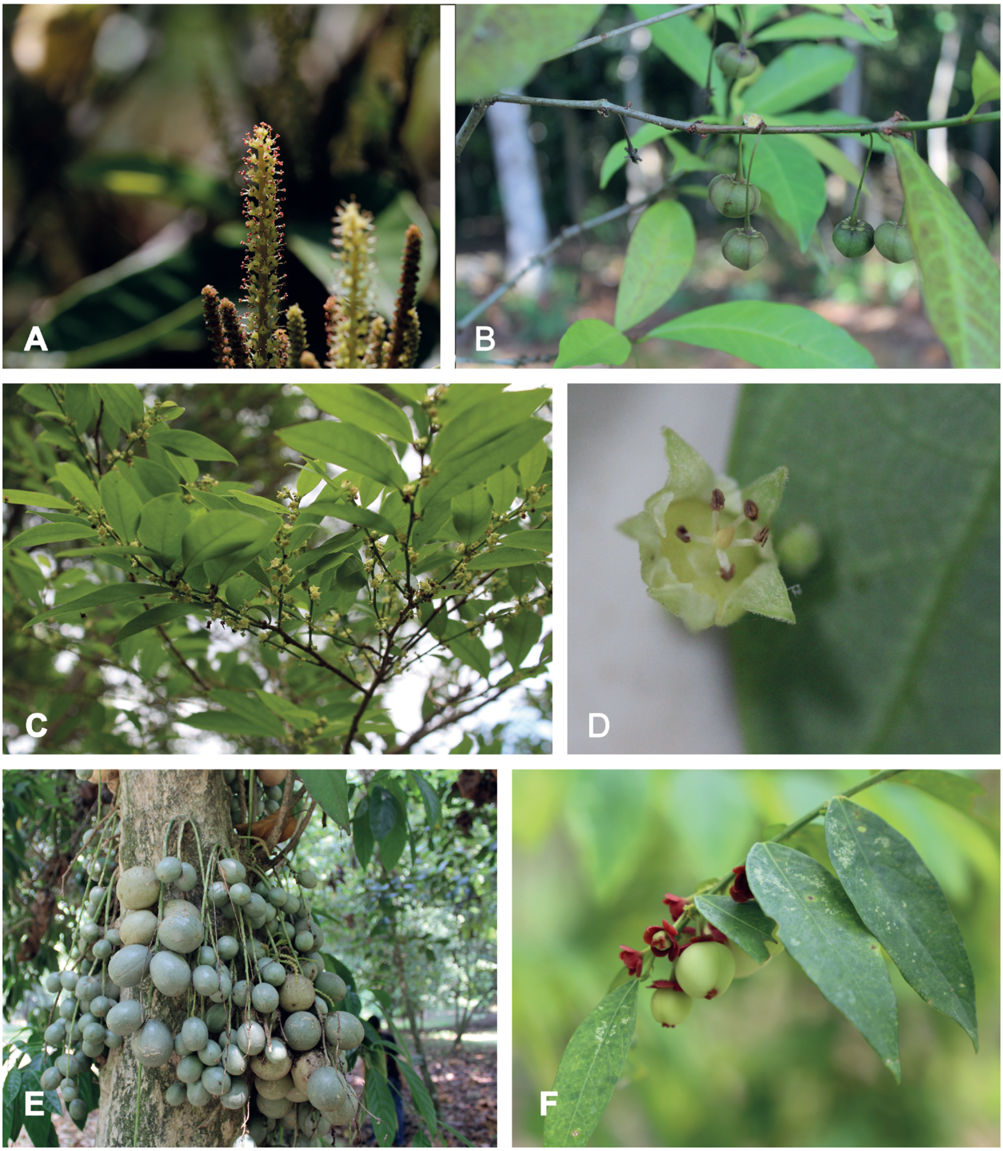


Figure 1-1. Examples of species of Phyllanthaceae: A. Flowers of *Antidesma bunius* (L.) Spreng., B. Fruits and flower of *Actephila excels* (Dalzell) Müll.Arg.; C. flowering branch of *Bridelia* sp.; D. close-up of a staminate flower of a *Bridelia* sp.; E. fruits of *Baccaurea macrocarpa* (Miq.) Müll.Arg.; F. pistillate flowers and fruits of *Breynia androgyna* (L.) Chakrab. & N.P.Balakr. Photos: A, B, C, D, E by R.W.Bouman; F by R.-Y. Yu.

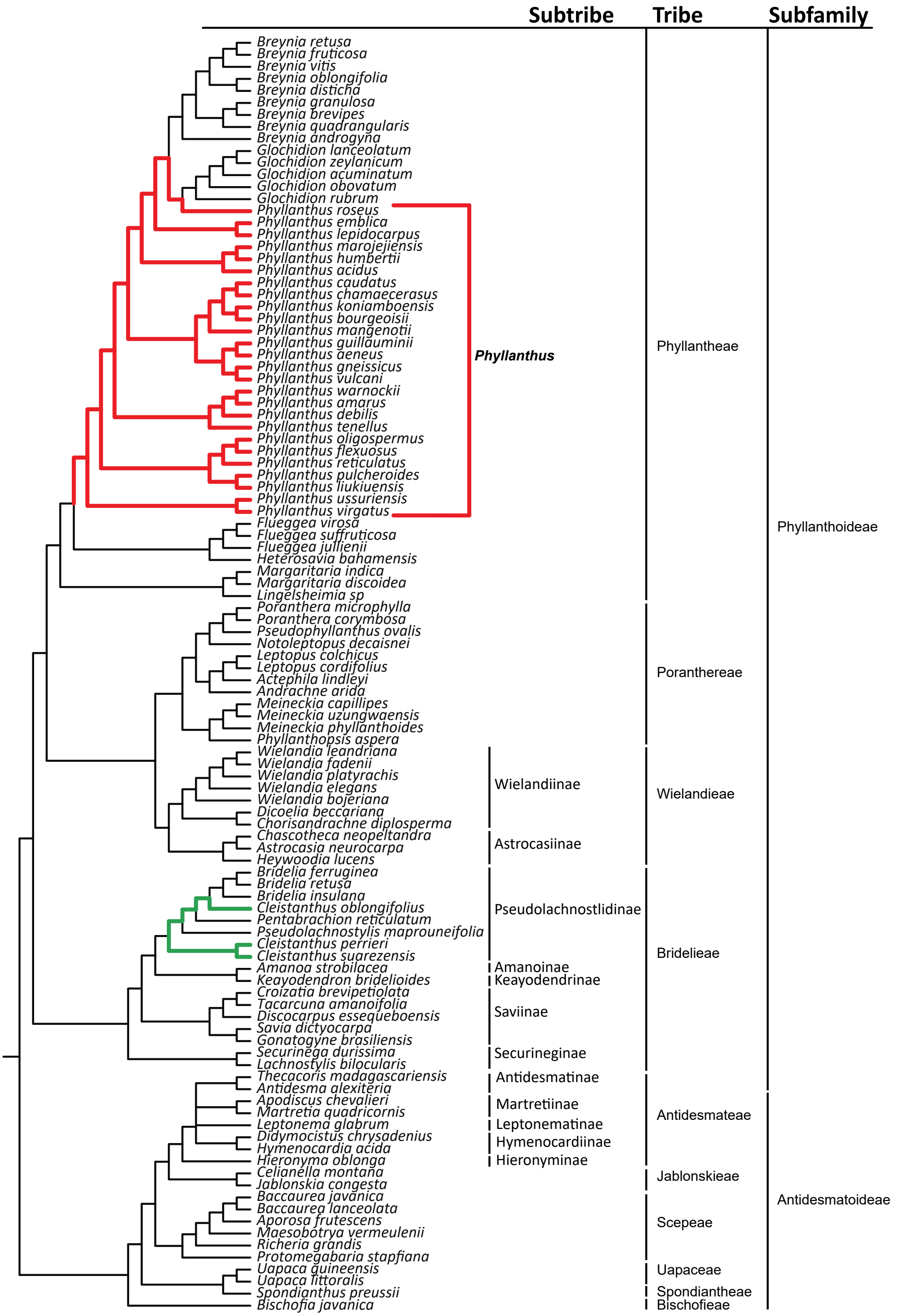
Table 1-1. Genera included in tribe Phyllantheae by different authors.

Dumort (1829)	Hoffmann et al. (2006)	Van Welzen et al. (2014a)
Cluytia	*Phyllanthus*	*Breynia*
Andrachne	*Flueggea*	*Flueggea*
Bridelia	*Phyllanthus*	*Glochidion*
Cicca	*Heterosavia*	*Heterosavia*
	Lingelsheimia	*Lingelsheimia*
Kirganelia	*Margaritaria*	*Margaritaria*
Xylophylla	*Plagiocladus*	*Plagiocladus*
Phyllanthus	*Phyllanthus*	*Phyllanthus*
	Phyllanthus	*Synostemon*

has changed considerably (Table 1-1). *Phyllanthus* was defined as a broad genus with more than 40 sections (Müller 1863, 1865, 1866). Subsequent changes reinstated *Glochidion* (Kurz 1873) and *Margaritaria* (Webster 1957, 1979) as distinct genera. In the phylogenetic classification by Hoffmann et al. (2006), tribe Phyllantheae was divided into a limited number of genera and the authors recommended to combine a paraphyletic *Phyllanthus* with the genera *Breynia* J.R.Forst. & G.Forst., *Sauropus* Blume and *Glochidion*. However, some feel that this would push taxonomic problems with *Phyllanthus* to the subgeneric level while still not resolving them (Pruesapan et al. 2012; van Welzen et al. 2014a).

Phyllanthus represents an interesting paraphyletic taxon with a rich taxonomical history, divergent morphology and practically unknown ecology. In this thesis I hope to address several interesting questions in *Phyllanthus* while exploring the evolution of this diverse genus. Coincidentally, problems in the classification of *Phyllanthus* is not limited to only plants as it was also the name of a genus of birds (Cibois et al. 2018)). This monospecific genus has been recently subsumed (Cibois et al. 2018) in the larger (formerly paraphyletic) genus *Turdoides* Cretzschmar 1826 (Leiothrichidae). While problems are probably not attached to the name itself, it remains a peculiar coincidence.

Figure 1-2. Molecular phylogeny of Phyllanthaceae resulting from Bayesian and Maximum likelihood analysis on the dataset of Kathriarachchi et al. (2005). Subtribes, tribes and subfamilies follow Hoffmann et al. (2006) but genera of tribe Poranthereae incorporate changes from Vorontsova & Hoffmann (2008). The paraphyly of *Phyllanthus* is highlighted in red and polyphyly of *Cleistanthus* is highlighted in green. Figure shown on adjacent page.


Subtribe
Tribe
Subfamily
Breynia retusa
Breynia fruticosa
Breynia vitis
Breynia oblongifolia
Breynia disticha
Breynia granulosa
Breynia brevipes
Breynia quadrangularis
Breynia androgyna
Glochidion lanceolatum
Glochidion zeylanicum
Glochidion acuminatum
Glochidion obovatum
Glochidion rubrum
Phyllanthus roseus
Phyllanthus emblica
Phyllanthus lepidocarpus
Phyllanthus marojejiensis
Phyllanthus humbertii
Phyllanthus acidus
Phyllanthus caudatus
Phyllanthus chamaecerasus
Phyllanthus koniamboensis
Phyllanthus bourgeoisii
Phyllanthus mangenotii
Phyllanthus guillauminii
Phyllanthus aeneus
Phyllanthus gneissicus
Phyllanthus vulcani
Phyllanthus warnockii
Phyllanthus amarus
Phyllanthus debilis
Phyllanthus tenellus
Phyllanthus oligospermus
Phyllanthus flexuosus
Phyllanthus reticulatus
Phyllanthus pulcheroides
Phyllanthus liukiuensis
Phyllanthus ussuriensis
Phyllanthus virgatus
Flueggea virosa
Flueggea suffruticosa
Flueggea jullienii
Heterosavia bahamensis
Margaritaria indica
Margaritaria discoidea
Lingelsheimia sp
Poranthera microphylla
Poranthera corymbosa
Pseudophyllanthus ovalis
Notoleptopus decaisnei
Leptopus colchicus
Leptopus cordifolius
Actephila lindleyi
Andrachne arida
Meineckia capillipes
Meineckia uzungwaensis
Meineckia phyllanthoides
Phyllanthopsis aspera
Wielandia leandriana
Wielandia fadenii
Wielandia platyrachis
Wielandia elegans
Wielandia bojeriana
Dicoelia beccariana
Chorisandrachne diplosperma
Chascotheca neopeltandra
Astrocasia neurocarpa
Heywoodia lucens
Bridelia ferruginea
Bridelia retusa
Bridelia insulana
Cleistanthus oblongifolius
Pentabrachion reticulatum
Pseudolachnostylis maprouneifolia
Cleistanthus perrieri
Cleistanthus suarezensis
Amanoa strobilacea
Keayodendron bridelioides
Croizatia brevipetiolata
Tacarcuna amanoifolia
Discocarpus essequeboensis
Savia dictyocarpa
Gonatogyne brasiliensis
Securinega durissima
Lachnostylis bilocularis
Thecacoris madagascariensis
Antidesma alexiteria
Apodiscus chevalieri
Martretia quadricornis
Leptonema glabrum
Didymocistus chrysadenius
Hymenocardia acida
Hieronyma oblonga
Celianella montana
Jablonskia congesta
Baccaurea javanica
Baccaurea lanceolata
Aporosa frutescens
Maesobotrya vermeulenii
Richeria grandis
Protomegabaria stapfiana
Uapaca guineensis
Uapaca littoralis
Spondianthus preussii
Bischofia javanica
Phyllanthus
Wielandiinae
Astrocasiinae
Pseudolachnostlidinae
Amanoinae
Keayodendrinae
Saviinae
Securineginae
Antidesmatinae
Martretiinae
Leptonematinae
Hymenocardiinae
Hieronyminae
Phyllantheae
Porantheae
Wielandieae
Bridelieae
Antidesmateae
Jablonskieae
Scepeae
Uapaceae
Spondiantheae
Bischofieae
Phyllanthoideae
Antidesmatoideae

Morphological diversity

With over 800 species (Chapter 3) originating from several evolutionary lineages, the genus *Phyllanthus* displays an enormous diversity of morphological characters (Fig. 1-3). Important characters within the genus and the rest of the tribe are the habit, branching system, flowers, fruits, seeds and pollen morphology.

The majority of species of *Phyllanthus* are woody plants varying from trees to shrubs, however herbaceousness has evolved several times independently (Chapter 7). Some well-known herbaceous species of *Phyllanthus* like *P. amarus* Schumach. & Thonn. and *P. urinaria* L. are often difficult to identify, which is complicated even more as a number of species have wide distributions and are invasive in many countries. By comparison, species of *Breynia* and *Glochidion* are usually shrubs to trees, while species of *Synostemon* F.Muell. are usually lower sprawling shrubs.

About 80% of the species of *Phyllanthus* exhibit a specialized branching system, which was coined by Webster (1956) as phyllanthoid branching. In this system, plagiotropic ultimate axes (side branches) resemble pinnate leaves, because they are deciduous and have a limited growth. These lateral branchlets are floriferous and bear laminate leaves while they are subtended by a scale-like leaf (cataphyll) and two cataphyllary stipules. Orthotropic axes typically only display laminate leaves in the first few nodes and switch to reduced leaves subtending the lateral axes in the upper nodes. Phyllanthoid branching is not present in *Phyllanthus* subgenera *Isocladus* G.L.Webster, *Macraea* (Wight) Jean F.Brunel and *Ceramanthus* (Hassk.) Jean F.Brunel, which are sister to the other clades in the genus (Kathriarachchi et al. 2006; Falcón Hidalgo et al. 2020) and it has been independently lost in several taxa (Chapter 6/7).

Inflorescences in *Phyllanthus* are generally axillary fascicles, unisexual or bisexual, with a varying number of flowers. Some taxa have more elaborate inflorescence structures like racemes (e.g. *Phyllanthus* subgenus *Gomphidium* (Baill.) G.L.Webster section *Nymania* (K.Schum.) J.J.Sm.) or thyrses (e.g. *Phyllanthus* subgenus *Xylophylla* section *Epistylium* (Sw.) Griseb.). The flowers show a relatively remarkable variation in form even though they consist of only a few elements. Flowers of *Phyllanthus* are characterized by two whorls of tepals (with some discussion on the differentiation of sepals and petals, see Gama et al. 2016), a (nectar) disc and either the andro- or gynoecium. The sepal number often differs between staminate and pistillate flowers and varies per subgenus. Pistillate discs are usually entire (with exceptions) and variable in size, while staminate discs are more often segmented with varying shapes. No studies have focused on the nectar production of these flowers and how the sugar composition looks like.

Micromorphological characters have had a large influence on the classification of *Phyllanthus*. Webster's (1956, 1957, 1958) seminal work on the

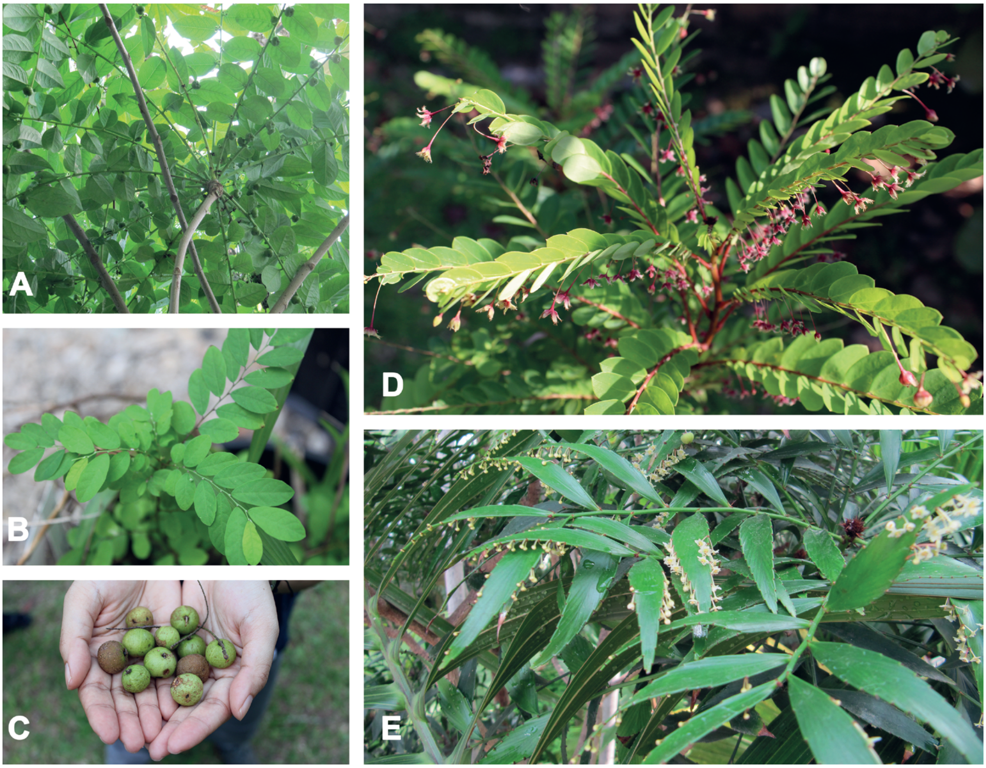


Figure 1-3. Examples of various species of *Phyllanthus*: A. *Phyllanthus juglandifolius* Willd. in fruit: B. *Phyllanthus Tenellus* Roxb.; C. fruits of *Phyllanthus emblica* L.; D. *Phyllanthus pulcher* Wall. ex Müll.Arg. in flower; E. *Phyllanthus arbuscula* (Sw.) J.F.Gmel. showing its characteristic phylloclades with flowers along the margins. Photos by R.W.Bouman.

infrageneric classification of *Phyllanthus* was expanded upon and complemented with a series of palynological studies from various authors (e.g. Punt 1967, 1972, 1975, 1980; 1987; Brunel 1987; Lobreau-Callen et al. 1988; Webster & Carpenter 2002, 2008; Sagun & van der Ham 2003; Santiago et al. 2004; Chen et al. 2009; Wu et al. 2016).

Similar to other taxa in Phyllanthaceae and Euphorbiaceae, most species of *Phyllanthus* are characterized by small schizocarpic fruits. Ornamentation and number of locules may be differentiative characters between species, but often the fruit morphology is similar between species. Drupaceous fruits have evolved independently in a few taxa and are mainly found in *Phyllanthus* subgenus *Kirganelia*, while some species are also cultivated for their edible fruits (e.g. *P. acidus* (L.) Skeels and *P. emblica* L.). The seeds are usually trigonal, but show differences between subgenera in their ornamentation.

Ecology and geography

Phyllanthus species can be found in a wide range of areas from a few desert species to the tropics. Only some invasive species are recorded in Mediterranean climate. The distribution of *Phyllanthus* and related genera has not been studied in detail. Early investigations based on the subgeneric classification from Webster (1956, 1957, 1958) indicated multiple dispersal events between continents (Holm-Nielsen 1979), but these have not been studied in a phylogenetic context. Similarly, while elevation or substrate is sometimes noted on collection labels, this has not been correlated between species or to specific distributions. Some well known calciferous species are known, but for example the amount of rheophytes is probably highly underestimated.

With the remarkable diversity in floral characters such as flower shape (open and disc-like to more closed and tube-shaped), disc shape and the variation in fusion and numbers of stamens and sepals, the cause could be inferred from pollination. Various systems are found and the ancestral system has been hypothesized based on observations in *Flueggea* (basal in the phylogeny) to be generalist bees or flies (Kawakita 2010). Kato et al. (2003) discovered a fascinating pollination system in *Glochidion*, which involves a mutualism with parasitic moths of the genus *Epicephala* Meyrick 1880. The female moths actively gather pollen from staminate flowers and visit pistillate flowers to pollinate them, afterwards they lay an egg in the flower and the developing larvae consume a portion of the seeds and receive protection from the plant. Host specificity and a close relation between plant and moth species are hypothesized to have caused a rapid co-evolution in *Glochidion* (see also Hembrey et al. 2013, 2018) and variations on this system are found in *Breynia* (Kawakita & Kato 2004b; Zhang et al. 2012) and various clades in *Phyllanthus* (Kawakita et al. 2009, 2019; Luo et al. 2011b; Kawakita & Kato 2017). This area of study is being further explored in terms of floral scent (Svensson et al. 2010), flower abortion (Goto et al. 2010), sharing and selection of hosts (Zhang et al. 2012) and seems to explain part of the rapid speciation of *Glochidion*. Similarly, in *Phyllanthus* this system has been related to the high species number found in subgenus *Gomphidium* (>100) which occurs mainly in New Caledonia, Australia and Papua New Guinea (Kawakita & Kato 2004a). However, comparable species numbers are not found in every clade associated with *Epicephala* moths and other factors should probably be included (Chapter 8).

As most species of *Phyllanthus* are characterized by schizocarpic fruits, the seeds are mostly dispersed autochorously. However, this mechanism and the distances traveled by seeds have not been studied for *Phyllanthus*. There are some indications that small fruits can disperse seeds about one to two meters (personal observation), but this has not been appropriately tested in the lab or the field. Similarly, dormancy of seeds has been a neglected study within the genus, but the presence of several invasive species suggests they can establish readily with an appropriate travel vector. Fleshy fruits have evolved several times independently within tribe Phyllantheae (Chapter7) and these are probably mostly dispersed by birds. Observations of bird dispersal have been sporadic in *Flueggea*, but has not been published for *Phyllanthus*. Similarly in *Glochidion*, the fruits dehisce to expose seeds with a brightly colored sarcotesta that is probably attractive to avian dispersers.

An interesting facet of a few species is their adaptation to areas with high metal concentrations in the ground. Recent studies in the biological accumulation of metals in plants have identified several species of *Phyllanthus* (Van der Ent et al. 2013; Nkrumah et al. 2016), which occur in ultramafic areas.

Genetics

Molecular systematics of *Phyllanthus* have mostly focused on resolving the relation between various taxa both at or above species level. First indications of paraphyly were found by Wurdack et al. (2004) and were subsequently confirmed by Samuel et al. (2005) and Kathriarachchi et al. (2006). Hoffmann et al. (2006) based an updated classification of Phyllanthaceae on the phylogeny from these previous studies. A molecular study of tribe Poranthereae and subsequent changes in classification on the groupings resulted in the recognition of eight genera (Vorontsova et al. 2007; Vorontsova & Hoffmann 2009). Pruesapan et al. (2008, 2012) argued that the classification of Hoffmann et al. (2006) would push taxonomic problems only to subgeneric levels while in turn creating a giant heterogeneous *Phyllanthus*. Increased sampling efforts of tribe Phyllantheae with a focus on *Breynia* and *Sauropus*, suggested that they should be combined, but could be kept separate from *Phyllanthus* while also reinstating the genus *Synostemon*. Full plastome sequences are only available for four taxa of tribe Phyllantheae: *Glochidion chodoense* C.S.Lee & Im(Cheon et al. 2019), *Flueggea virosa* (Roxb. ex Willd.) Baill. (Wang et al. 2020), *Breynia fruticosa* (L.) Müll. Arg. (Zhou et al. 2020) and *P. emblica* (record NC_047477.1 on Genbank). There are some indications of a possible genome duplication occurring in tribe Phyllantheae, but data on chromosomal numbers or genome sizes are severely lacking for many taxa (see Webster & Ellis 1962). Sampling of *Phyllanthus* has previously covered about 10% of the genus, but some subgenera and sections have not yet been included. A more thorough sampling could investigate the relationship between major lineages of *Phyllanthus* and test the monophyly of the current classification of subgenera and (sub) sections within the genus.

Medicinal effects and metabolites

Two species are common in cultivation because they are renowned for their edible fruits (*P. acidus* and *P. emblica*), which are high in vitamin C (Liu et al. 2008). Aside from their nutritional value, a long list of species are also used in traditional medicine or hunting practices (Unander et al. 1990, 1991, 1992, 1995), however only a small number of species have been included in studies towards bioactive compounds. This is where botanical gardens, which harbour an enormous diversity of plant species, provide an opportunity to study more species.

Outline and aims of this thesis

Several gaps in knowledge have been highlighted in the introduction above, the largest of which is the current paraphyly of the genus *Phyllanthus*. With this thesis, I aim to expand our knowledge of *Phyllanthus* and discuss broader evolutionary patterns in the context of their morphology and phylogenetics. To begin studying the diversity within *Phyllanthus*, which has been described across hundreds of papers, this information needed to be summarized and the system of subgenera and sections was an ideal candidate that needed to be applied to the rest of *Phyllanthus* (Chapter 2 & 3). From this review, several taxonomic problems were identified and some subsequently treated (Chapter 4 & 5). With the rising use of *Phyllanthus* in traditional medicine, we wished to test several lineages for their bioactive compounds, to identify possible further interesting groups (Chapter 6). As the classification was based on morphology, we wanted to expand the current sampling for phylogenetic studies of *Phyllanthus* to see whether all groups were monophyletic (Chapter 7). The phylogeny allowed us to map broad distribution patterns of various clades and study where *Phyllanthus* originated and how it dispersed to the rest of the world (Chapter 8). Finally, a decision needed to be made on the paraphyly of *Phyllanthus*, which will have taxonomic consequences for an enormous amount of species (Chapters 9).

Chapter 2

In the preparation of this thesis, several new species of *Phyllanthus* were discovered through herbarium or molecular work. *Phyllanthus rufuschaneyi* Welzen, R.W.Bouman & Ent is the first to be described (Bouman et al. 2018a) and its general affinities are discussed. What makes this species all the more interesting, is the fact that it was grown at Kinabalu parks (Sabah, N. Borneo) for several years and studied for its extraordinary accumulation of metals. Therefore, this species is a strong candidate for its use in the upcoming field of agromining, which aims to use plants for the collection of metals from contaminated soils or those naturally rich in heavy metals.

Chapter 3

Breynia, *Synostemon* and *Glochidion* were found to be nested within *Phyllanthus*, but the genera were upheld by van Welzen et al. (2014a). *Phyllanthus* is therefore a paraphyletic genus and to explore whether it is possible to split the genus, each species needs to be placed in a morphological and phylogenetic framework. In chapter 3, a table is presented that summarizes the taxonomic history of *Phyllanthus* and updates the classification system to cover all accepted species(Bouman et al. 2018b). Several taxonomic problems are highlighted for future study and a provisional key to the subgeneric classification of *Phyllanthus* is provided.

Chapter 4

One of the remaining taxonomical anomalies presented in chapter 3 concerns *Phyllanthus* subgenus *Isocladus* and its originally broad treatment by Webster (1956). Following his treatment would result in a polyphyletic subgroup, but the alternative, a classification by Brunel (1987) has often been ignored. Subgenus *Macraea* was originally placed in subgenus *Isocladus*, but was shown to be phylogenetically distinct (Kathriarachchi et al. 2006). This group of plants is here revised over its entire distribution and its taxonomic rank and affinity are discussed extensively to highlight morphological (dis)similarities with other plants of the genus *Phyllanthus*.

Chapter 5

Due to a lack of material and incomplete descriptions, not all species could be confidently assigned in chapter 3 to a specific subgeneric group. Two species were described by Koorders (1904) for the island of Sulawesi (Indonesia), but the initial description only mentioned the habit and which species it resembled. With no mention of the morphology of the flowers, the affinity of these species was initially unknown. During a recent trip during a Flora Malesiana Symposium in the region, I had the chance to see type material collected by Koorders himself that is currently stored at the herbarium of Bogor (BO) in Cibinong (Java, Indonesia). In a short revision, which includes flower descriptions, these species are assigned to *Phyllanthus* subgenus *Erioccous* and their closest affinity seems to be to species that occur in the Philippines. The biogeographical implications are discussed and a key to the species of *Phyllanthus* on Sulawesi is presented. As Sulawesi remains drastically understudied, this small contribution opens the path to finding new species.

Chapter 6

To further explore the medicinal effects of various species of *Phyllanthus*, I sampled material from the living collections of the Hortus botanicus Leiden and studied their antimicrobial and antifungal effects in correlation with their metabolite content. Some species were found to have antimicrobial effects, but we could not determine which compounds were responsible for this.

Chapter 7

As past morphological work resulted in classifications that were not strictly monophyletic, the framework presented in chapter 3 needs to be complemented with a phylogeny with adequate sampling. The previous phylogenetic study that focused on *Phyllanthus* (Kathriarachchi et al. 2006) included about 10 % of the whole genus. Increased sampling efforts by Pruesapan et al. (2008, 2012) already elucidated the structure of the genus *Breynia* (with *Sauropus* found to be nested within). Here, I increased the sampling efforts for the genus *Phyllanthus* itself in an attempt to include the majority of morphological variation and to add some understudied areas such as Australia. With increased sampling, I hope to confirm how *Phyllanthus* can be split in monophyletic genera and how they can be morphologically recognized.

Chapter 8

Most of the work on this thesis has been geared towards the goal of creating a new classification for the genus *Phyllanthus*. Here together with experts of different floras, we incorporate the results from all previous chapters into a new classification of tribe Phyllantheae. In this chapter I reinstate several genera to create a new classification of monophyletic taxa, some with a more restricted distribution. This new classification shows that *Phyllanthus* is restricted to the neotropics with only some cultivated species more widely distributed. With this, we propose a possible solution to the problem of paraphyly within the tribe.

Chapter 9

Now turning from taxonomy to its distribution, another aspect of why *Phyllanthus* is so remarkable is studied in this chapter. *Phyllanthus* occurs in all tropics and subtropics with a few species reaching temperate areas. However, how this distribution came to be has never been explored extensively. Initial surveys that incorporated older subgeneric classifications were minimal and only an extensive discussion existed for Africa, which did not incorporate any phylogenetics. By using the phylogeny of chapter 7 in conjunction with an expanded dataset of the distribution of included species and a dataset of fossil findings, we calibrate the phylogeny to determine how old the nodes on the phylogenetic tree are and reconstruct how the group might have reached its current distribution. By analysing this, I hope to correlate this with known events of plate tectonics and environmental conditions that could have allowed for the dispersal and colonization of new areas by the genus through time.

Chapter 10 General conclusions

In the last chapter of this book, I discuss the knowledge gained on tribe Phyllantheae and its evolution and diversification. New problems are still created and several areas remain poorly studied for this interesting group of species. With a new appreciation of each individual clade and its new constituent genera, new problems are highlighted that offer interesting case studies for several evolutionary subjects. Some considerations are presented that would serve as a continuation of this work.

CHAPTER 2

Phyllanthus rufuschaneyi: a new nickel hyperaccumulator from Sabah (Borneo Island) with potential for tropical agromining

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Published in Botanical Studies 59 (9):1 - 12. 2018

https://doi.org/10.1186/s40529-018-0225-y

Chapter 2

Phyllanthus rufuschaneyi: a new nickel hyperaccumulator from Sabah (Borneo Island) with potential for tropical agromining

Short title: A new nickel hyperaccumulator from Sabah

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Abstract

Nickel hyperaccumulator plants are of much interest for their evolution and unique ecophysiology, and also for potential applications in agromining—a novel technology that uses plants to extract valuable metals from soil. The majority of nickel hyperaccumulators are known from ultramafic soils in tropical regions (Cuba, New Caledonia and Southeast Asia), and one genus, *Phyllanthus* (Phyllanthaceae), is globally the most represented taxonomic entity. A number of tropical *Phyllanthus*-species have the potential to be used as 'metal crops' in agromining operations
mainly because of their ease in cultivation and their ability to attain high nickel concentrations and biomass yields. One of the most promising species globally for agromining, is the here newly described species *Phyllanthus rufuschaneyi*. This species can be classified in subgenus *Gomphidium* on account of its staminate nectar disc and pistillate entire style and represents the most western species of this diverse group. The flower structure indicates that this species is probably pollinated by Epicephala moths. *Phyllanthus rufuschaneyi* is an extremely rare taxon in the wild, restricted to Lompoyou Hill near Kinabalu Park in Sabah, Malaysia. Its utilization in agromining will be a mechanism for conservation of the taxon, and highlights the importance of habitat and germplasm preservation if rare species are to be used in novel green technologies.

Keywords: Epicephala pollination, Nickel hyperaccumulation, Phyllanthaceae, *Phyllanthus* subgenus *Gomphidium*, Sabah

Introduction

Whereas the great majority of plants growing on naturally nickel (Ni) rich ultramafic soils exclude it from uptake and translocation, a minority of plants display a highly unusual response with enhanced uptake and transfer to the shoots (Reeves 2003; Van der Ent et al. 2013a). These plants are called 'hyperaccumulators' and they have the ability to accumulate trace elements to extreme concentrations in their living tissues (Jaffré et al. 1976; Van der Ent et al. 2013a). The Ni concentrations in some species can reach up to 16.9 Wt% in the phloem sap (Van der Ent and Mulligan 2015). Although there are over 400 known Ni hyperaccumulators species (> 0.1 Wt% shoot dry weight), there are just ca. 50 *hypernickelophores* (e.g. hyperaccumulator species with > 1 Wt% Ni shoot dry weight) known globally (Reeves 2003; Reeves et al. 2017). Hyperaccumulator plants can be used as 'metal crops' in agromining (phytomining) operations to generate metal-rich biomass for commercial gain (Chaney et al. 1998; Van der Ent et al. 2015a). This innovative approach enables access to resources not accessible by conventional mining techniques such as abundant lowgrade sources of valuable elements (Li et al. 2003; Van der Ent et al. 2015a). Agromining can also benefit local communities, by providing new income opportunities for farmers in developing countries (Bani et al. 2015; Chaney et al. 2018). The greatest potential for agromining is in tropical regions (Cuba, New Caledonia and Southeast Asia) where some of the world's largest low-grade nickel sources are located (Van der Ent et al. 2013b).

On a global scale, Ni hyperaccumulation occurs most frequently in the order Malpighiales, particularly in the families Dichapetalaceae, Phyllanthaceae, Salicaceae and Violaceae.

The Phyllanthaceae has the greatest numbers of hyperaccumulators with representatives in the genera *Actephila* Blume, *Antidesma* L., *Breynia* J.R.Forst. & G.Forst., *Cleistanthus* Hook.f. ex Planch., *Glochidion* J.R.Forst. & G.Forst. and *Phyllanthus* L. The latter is pantropical and the most speciose genus of the family with over 800 species globally (Govaerts et al. 2000; Kathriarachchi et al. 2006; Bouman et al. under review). Due to its great diversity in morphology, *Phyllanthus* is currently classified in many subgenera and (sub)sections, which were often former separate genera. The genus is characterized by its unisexual flowers, the absence of petals and a characteristic branching system called phyllanthoid branching (see Fig. 2-2a; Webster 1956). Species with this particular type of branching have deciduous, plagiotropic branchlets that are subtended by reduced scale-like leaves (cataphylls) (Webster 1956). Normal leaves and flowers are only found on the plagiotropic branchlets. This branching system has been lost several times (Kathriarachchi et al. 2006) and in species with non-phyllanthoid branching, leaves can be found on all axes and the branchlets are not deciduous and subtended by normal leaves. The genus *Phyllanthus* is currently paraphyletic with the genera

Breynia, *Glochidion* and *Synostemon* F.Muell. nested within (Kathriarachchi et al. 2006; Pruesapan et al. 2012). Discussions on how to resolve the paraphyly of the genus *Phyllanthus* are still ongoing (see Hoffmann et al. 2006; Van Welzen et al. 2014a). One of the most speciose subgenera is subgenus *Gomphidium* (Baill.) G.L.Webster. Species in the subgenus are characterised by phyllanthoid branching in combination with flowers with biseriate sepals, stamens with free filaments (but connate in one section) and three duplex nectar glands (sometimes divided and then 6 or absent). The phylogenetic position of subgenus *Gomphidium* was not consistent between the markers used in the study of Kathriarachchi et al. (2006) and requires further study.

Major centres of diversity for *Phyllanthus* are in New Caledonia with over 100 species of which 15 species are Ni hyperaccumulators (Kersten et al. 1979; Schmid 1991; Jaffré et al. 2013), in Cuba with at least 40 species of which 17 species are Ni hyperaccumulators (Leon and Alain 1953; Reeves et al 1996), and in the Malesian Region about 100 species of which 5 species are Ni hyperaccumulators (Van der Ent et al. 2015a, b, c; Wu et al. 2016; Galey et al. 2017).

A number of taxa in the genus *Phyllanthus* are among the most promising 'metal crops' due to their fast growth and other favourable growth characteristics, including easy propagation and pest resistance (Nkrumah et al. 2016). Some *Phyllanthus*-species also reach some of the highest Ni concentrations known in any hyperaccumulator plants, with 3.8 Wt% in the leaves of *P. serpentinus* S.Moore from New Caledonia (Jaffré 1977; Kersten et al. 1979; as *P. favieri* M.Schmid), 3.9 Wt% in the leaves of *Phyllanthus insulae-japen* Airy Shaw from Indonesia (Reeves 2003), and 6 Wt% in the leaves *P.* × *pallidus* C.Wright ex Griseb. from Cuba (Reeves et al. 1996).

Further study of other genera within the Phyllanthaceae continues to yield new Ni hyperaccumulator records, such as in the genus *Antidesma* (Nkrumah et al. 2018), and even new species that are hyperaccumulators, such as the recently described *Actephila alanbakeri* Welzen & Ent (Van der Ent et al. 2016a). Kinabalu Park is the world's most species-rich hotspot with over 5000 species in 1000 genera and 200 families recorded to date (Beaman and Beaman 1990; Beaman 2005) of which 2542 plant species have been found on the ultramafic soils inside the Park (Van der Ent et al. 2015c). In Sabah, a total of 8 species of *Phyllanthus* occur, of which two are known Ni hyperaccumulators: *P. balgooyi* Petra Hoffm. & A.J.M.Baker which can accumulate up to 1.6 Wt% Ni in the leaves and up to 16.9 Wt% Ni in the phloem sap and the here newly described *Phyllanthus rufuschaneyi* (Hoffmann et al. 2008; Van der Ent and Mulligan 2015; Mesjasz-Przybylowicz et al. 2016). *Phyllanthus balgooyi*, also occurs in the Philippines, in addition to *Phyllanthus securinegioides* Merr. (which can accumulate up to 3.5 Wt% in the leaves), and a third Ni hyperaccumulator species from the genus, *P. erythrotrichus* C.B.Rob. which can accumulate up to 1.1 Wt% Ni in the leaves (Baker et al. 1992; Quimado et al. 2015). The extreme levels of Ni accumulation in these species poses important questions about the ways in which these plants take up, transport and store Ni, while avoiding the potential effects of metabolic toxicity. In leaves, Ni appears to be associated mainly with organic acids, such as citrate, malate and malonate (Kersten et al. 1980; Homer 1991; Montargès- Pelletier et al. 2008; Van der Ent et al. 2017).

In early 2013, a hitherto unknown species of *Phyllanthus* was planted in the local garden by staff at the Monggis substation of Kinabalu Park. Spot-testing with dimethyl-glyoxime-impregnated paper revealed it to be a strong Ni hyperaccumulator, which was subsequently confirmed through Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES) on acid-digested samples of leaves in the laboratory (first reported in Van der Ent et al. 2013c). The plant was collected from an unknown location near the Kinabalu Park boundary and could not be re-collected at the time. In 2015, the taxon was 're-discovered' during fieldwork on Lompoyou Hill, approximately 12 km from Monggis substation, where it was locally abundant (Fig. 2-1). The taxon is of significant scientific interest because of the extremely high levels of Ni accumulation, reaching up to 2.8 Wt%

Figure 2-1. Different aspects of the habitat of *P. rufuschaneyi* in Sabah, Malaysia. A. Lompoyou Hill seen from Nalumad village; B. Garas—the eastern end of Lompoyou Hill, the outcropping ultramafic (serpentinite) bedrock is clearly visible in the road cuts; C. *Phyllanthus rufuschaneyi* growing in situ on Lompoyou Hill; D. the summit of Lompoyou Hill with secondary scrub and dead standing trees after forest fires. Photos by A. van der Ent.

Ni in leaves and 1.8 Wt% in the phloem tissue (Van der Ent and Mulligan 2015). Following its discovery, the ecophysiology was studied in detail, which revealed that Ni is mainly concentrated in the phloem in roots and stems, and in the leaves in the epidermis (Van der Ent et al. 2017). Apart from scientific interest, the taxon has great potential for agromining, which was studied in a pioneering nursery pot experiment and field trial (Nkrumah et al. 2016). This experimental work demonstrated that P. *rufuschaneyi* has advantageous characteristics for utilization as a 'metal crop' including fast growth rate, easy re-growth after coppicing, tolerance for exposed conditions on eroded soils and high Ni accumulation in its whole biomass. Taken together, P. *rufuschaneyi* has the best combination of characteristics of any tropical 'metal crop' presently known. The bio-ore (e.g. ashed biomass) of P. *rufuschaneyi* contains up to 12.7 Wt% Ni and the extractive hydrometallurgy of this material was studied for producing high-purity Ni salts for the electrochemical industry (Vaughan et al. 2017). At first, this plant was only known as *Phyllanthus* cf. *securinegioides* Merr. (and reported as such in Van der Ent et al. 2015b, 2016b, 2017), because of its superficial resemblance to this species from the Philippines. However, after examination of the literature and other specimens, we conclude that it is a new species that is of great interest for its taxonomic position and its qualities as a hyperaccumulator. Here we describe this taxon and provide information about its taxonomic relations, distribution, ecology, hyperaccumulation properties, and conservation status.

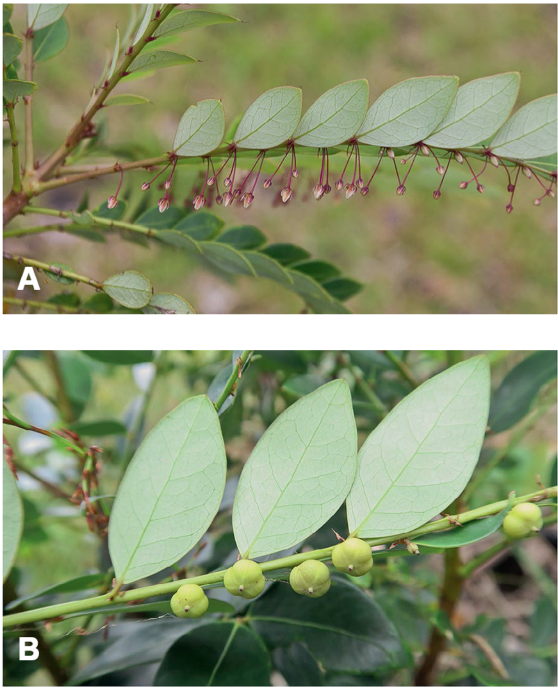

Figure 2-2. Detail of *P. rufuschaneyi* plants. A. inflorescences of *P. rufuschaneyi*, note the difference between main stem and side stem with at the base small structures that signal phyllanthoid branching; B. fruit capsules of *P. rufuschaneyi*. Photos by A. van der Ent.

Methods

Taxonomical investigation

The material studied comprised of herbarium specimens loaned from the Sabah Parks Herbarium (SNP) in Sabah, Malaysia. Descriptions were made using standard taxonomical techniques and morphological terminology follows Beentje (2016).

The IUCN conservation status was assessed applying the IUCN Red List Categories (IUCN 2001) that considers (i) extent of occurrence (EOO), and (ii) area of occurrence (AOO) in order to generate applicable IUCN threat categories.

Collection of plant samples for chemical analysis

Plant tissue samples (leaves, wood, bark, flowers) for bulk chemical analysis were collected in the habitat (6°06'29.6"N 116°47'36.7"E) near Kinabalu Park in Sabah, Malaysia. These samples were dried at 70 °C for 5 days in a drying oven and subsequently packed for transport to Australia and gamma irradiated at Steritech Pty. Ltd. In Brisbane following Quarantine Regulations in Australia. The dried plant tissue samples were subsequently ground and digested using 4 mL HNO_3 (70%) and 1 mL H_2O_2 (30%) in a microwave oven (Milestone Start D) for a 45-min programme and diluted to 30 mL with ultrapure water (Millipore 18.2 MΩ cm at 25 °C) before analysis with ICP-AES (Varian Vista Pro II) (Huang et al. 2004). The elemental concentrations originate from previously reported data (Van der Ent and Mulligan 2015; Van der Ent et al. 2015b, 2017) augmented with new data from plant tissue samples collected for this study.

Results

Taxonomic treatment

Phyllanthus rufuschaneyi Welzen, R.W.Bouman and Ent, sp. nov.—TYPE: MALAYSIA. Sabah, near Kampong Nalumad, eastern boundary Kinabalu Park, Lompoyou Hill, Antony Van der Ent et al. SNP 32987! (holo SNP; iso L). Paratype: SNP 22039!, Lompoyou Hill, Sabah, Malaysia (Figs. 2-2, 2-3, 2-4).

This species is most similar to *P. securinegoides* from the Philippines, from which it can be distinguished by its smaller leaves, staminate flowers with connate filaments and pistillate flowers with connate tubular stigmas.

Shrub to tree(let), up to 6 m high, monoecious, phyllanthoid branching present, main branches often hollow. *Indument* generally absent, on some parts asperities (stiff, short, papillae-like hairs) on orthotropic and plagiotropic branches and sometimes petioles and pedicels. *Plagiotropic branches* 1–1.5 mm wide, not flattened, with 2 narrow longitudinal wings, to 0.3 mm wide, asperities usually present between wings. *Stipules* ovate, 1.5–6 by 0.8–1 mm, persistent, becoming brown when dry, basally eared, ears sometimes elongated. *Leaves* distichous, simple, dimorphous (reduced on orthotropic branch to cataphylls (scale leaves), not reduced on plagiotropic branches). *Cataphylls* on main trunk below branches, stipule-like, ovate to triangular, c. 3 mm long, early caducous. *Leaves on plagiotropic* *branches* petiole more or less dorsoventrally flattened, 1–1.5 mm long, glabrous or with asperities, transversely wrinkled when dry; blade ovate to elliptic, 1.6–3.7 (without mucro) by 0.5–1.2 cm, 2.2–3.7 times longer than wide, coriaceous, base attenuate, asymmetric, margin entire, somewhat thickened, slightly revolute, apex rounded to acuminate, mucronate up to 5.2 mm, mucron usually breaking off, upper and lower surface glabrous, smooth, lower surface glaucous; venation pinnate, above hardly visible, slightly raised underneath, secondary veins 6–8 per side, looped and closed near margin, higher order veins reticulate. *Inflorescences* consisting of unisexual or bisexual fascicles, flowers 1–4 per node; staminate flowers single or a few, generally in lower axils but sometimes at end of branches, usually together with a single pistillate flower; latter also single in upper axils. *Staminate flowers* 1.4–2 mm diameter, remaining closed, actinomorphic; pedicel slender, 6.7–12 mm long, apically somewhat thickened; sepals 6, upright, tightly packed, margin entire, apex rounded; outer three smaller (when young) to slightly longer than inner ones, 1.9–2 by 0.9–1 mm, central part thickened, pink, margins and upper half thin, white to whitish pink; inner 3 1.4–2.3 by 1.3–1.4 mm, lower part almost naillike, central midrib area thickened and darker coloured, basal central part inside attached to androphore via a ^-like structure; disc lobes 6, paired, vertical, kidneylike, c. 0.6 mm long, greyish blue when dry, attached to broad part of flower receptacle, smooth; stamens 3, filaments connate, c. 1 mm high, broadly cone-shaped, apically with erect anthers, these elliptic, c. 0.7 by 0.4 mm, opening extrorse via lengthwise slits, apically on connective a c. 0.3 mm long slender appendix. *Pistillate flowers* 1.4–1.6 mm diameter, actinomorphic; pedicel 1–2 mm long, round, glabrous or with asperities; sepals 6, tight to ovary in flower, spreading in fruit, base very thickened, attached to receptacle, margin entire, outer 3 slightly smaller than inner 3, elliptic, 1.7–2 by c. 1 mm, apex truncate to erose, inner 3 elliptic, c. 2 by 1.2–1.6 mm, apex rounded; disc lobes 6, small, globose, less than 0.2 mm in diameter; gynophore c. 0.3 mm high, ovary ovoid, c. 1.3 by 1.1–1.3 mm, 3-locular, 2 ovules per locule, smooth, glabrous, three stigmas united into a cone of 0.8–1 mm high, apically somewhat erose (slightly split stigmas) and hollow inside. *Fruits* c. 7.5 mm in diameter, c. 4.5 mm high, opening completely septicidal and partly to completely loculicidal, exocarp separating from meso- and endocarp, wall thin, woody when dry, smooth, glabrous; columella broadly triangular, 2–2.3 mm high. *Seeds* ovoidtriangular, c. 2.8 by 1.8 mm, brown, smooth, not seen mature.

Etymology

The specific epithet "*rufuschaneyi*" honours Dr. Rufus L. Chaney (b. 1942), an agronomist who is widely credited for inventing phytomining (agromining) (Chaney 1983), leading to the technology being patented (Chaney et al. 1998). Dr. Chaney has worked for 47 years at the USDA Agricultural Research Service (USA) on risk assessment for metals in soils and crops, and the food-chain transfer and bioavailability of soil and crop metals to humans. He published over 490

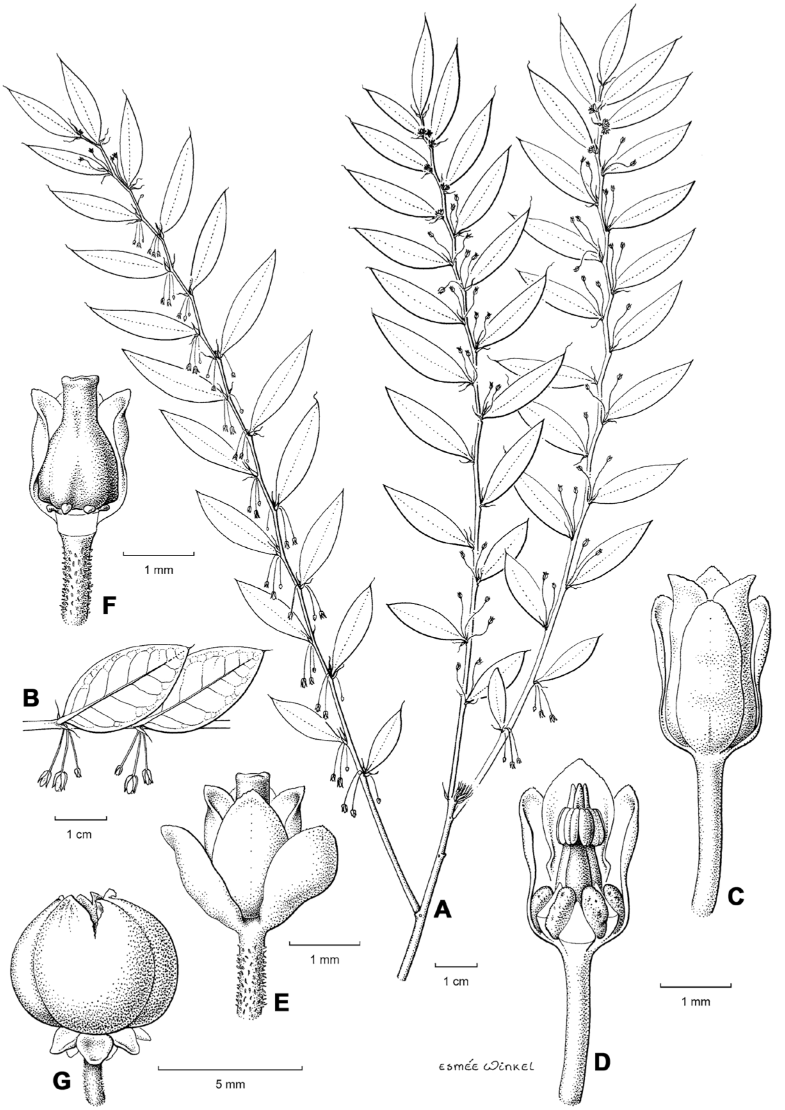

Figure 2-3. *Phyllanthus rufuschaneyi* Welzen, R.W.Bouman & Ent: A. a branch with only scars of cataphylls and cataphyllary stipules present at the base of branchlets as these are caducous (drawn from herbarium specimen with leaves glued sideways and staminate flowers sometimes upright instead of hanging); B. detail of sidebranch with leaves and staminate flowers in natural position; C. staminate flower; D. staminate flower with part of sepals removed showing disc glands and androecium; E. pistillate flower; F. pistillate flower with part of sepals removed showing disc glands and ovary; G. fruit (A, C, D *Daim Endau 225*; B *Lomudin Tadon g257*; E, F *SNP 32987*; G *Lomudin Tadon 257*; all SNP). Drawing by Esmée Winkel (2017).

publications and won the Gordon Award for Lifetime Achievement and Excellence in Phytoremediation Research. The fact that *P. rufuschaneyi* is the most promising tropical Ni 'metal crop' presently known, makes this recognition fitting.

Phenology and pollination

The species flowers and fruits all year round. Especially young plants growing in open habitats flower profusely on many branches. Flowering is less frequent when plants grow under more shaded conditions in developing forest. Many *Phyllanthus* species are pollinated by moths of the genus *Epicephala* Meyrick. Females of these moths actively pollinate the flowers and then deposit eggs into the floral ovaries, after which the larvae consume some of the developing seeds (Kawakita 2010). *Phyllanthus rufuschaneyi*, like all other species in subgenus Gomphidium, is likely pollinated by *Epicephala* moths (Kato and Kawakita 2017) as the staminate flowers are highly closed (inner sepals even grown together with the broad androphore) and possess vertical anthers, the pistillate flowers have grown together, cone-like, non-opening stigmas. Although pollination has not been specifically studied in this species, *Epicephala* larvae were observed in the fruit capsules of P. *rufuschaneyi* in the field. The similarity with Glochidion flowers, also pollinated by *Epicephala* moths, is remarkable. The co-evolution and high specificity for *Epicephala*-species for *Phyllanthus*-species has been linked to the extensive diversification of this genus in New Caledonia (Kawakita and Kato 2004a).

Distribution, habitat and ecology of Phyllanthus rufuschaneyi

Phyllanthus rufuschaneyi is known only from two populations; one (very small) population at the foot of Bukit Hampuan, and another larger population on Lompoyou Hill approximately 5 km from the first population. The habitat in both localities is open secondary scrub that has been affected by recurring forest fires (Fig. 2-1). Lompoyou Hill is close to the villages of Nalumad and Pahu. The hill (400 m asl) has been burnt at least once as a result of an uncontrolled forest fire in 1998. Prior to burning, the site was already disturbed by logging. The area has a short and open scrub community (dominated by shrubs 1–3 m tall) with pioneer species such as *Macaranga kinabaluensis* Airy Shaw (Euphorbiaceae). In this habitat type several other Ni hyperaccumulator plant species occur, including *Phyllanthus balgooyi*, *Actephila alanbakeri*, *Mischocarpus sundaicus* Blume (Sapindaceae), and *Xylosma luzonensis* Clos (Salicaceae). The local conditions are xeric, and the soils are shallow and heavily eroded with limited amounts of organic matter. In pot experiments *P. rufuschaneyi* responded negatively to increasing organic matter amendments (Nkrumah et al. 2017). *Phyllanthus rufuschaneyi* occurs exclusively on these young eroded soils (hypermagnesian Cambisols) that occur at low elevation (700 m asl) on strongly serpentinised bedrock. These soils have extremely high magnesium (Mg) to calcium (Ca), circum-neutral pH, and high available Ni as a result of the disintegration of phyllosilicates and re-sorption onto secondary iron (Fe)- oxides

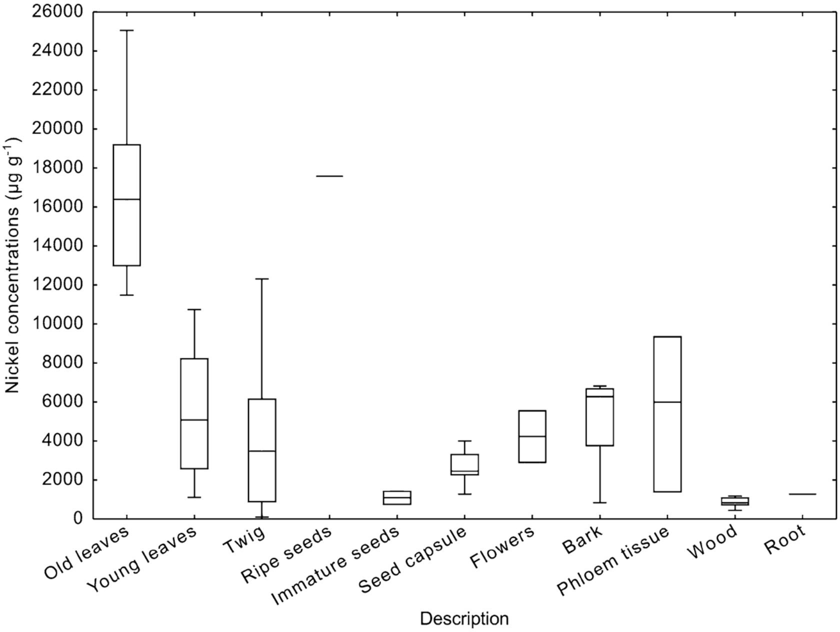

Figure 2-4. Elemental concentration in various plant parts of *P. rufuschaneyi*. Data from Tables 2-1 and 2-2.

or high-charge clays (Echevarria 2018). In Sabah, Ni hyperaccumulator plant species are restricted to these soils with a pH > 6.3 and relatively high total soil Ni concentrations > 630 µg g–1 (Van der Ent et al. 2016b).

Elemental concentrations in the plant tissues

Bulk elemental concentrations of macro-elements (mainly essential nutrients) are given in Table 1; Fig. 2-4. Aluminium (Al) concentrations are uniformly low in all plant parts, but highest in the flowers (up to 370 µg g^{-1}). Calcium is high to extremely high in many parts of the plant, especially in the old leaves (up to 1.09 Wt%), in the bark (up to 2.34 Wt%) and in the twigs (up to 2.59 Wt%). Potassium (K) concentrations are remarkably high for a plant species growing on severely K-deficient soils. The highest K concentrations are in the old leaves (up to 1.34 Wt%) and twigs (up to 1.37 Wt%), and the lowest in the roots (53 µg g^{-1}). Magnesium concentrations are particularly high in the immature seeds (mean of 4931 µg g^{-1}). Sodium (Na) concentrations are unremarkable, but highest in the young leaves with up to 2325 µg g^{-1} (mean is 390 µg g^{-1}). Finally, sulfur (S) concentrations vary widely with the lowest concentrations in the roots (81 µg g^{-1}) and the highest in the immature seeds (up to 3290 µg g^{-1}).

Bulk elemental concentrations of trace-elements (transition group elements) are

Table 2-1. Elemental concentration (macro elements: Al, Ca, K, Mg, Na, P, S) ranges and means in parentheses.

Plant part	*N* samples	Al	Ca	K	Mg	Na	P	S
Flowers	2	20–370 [195]	1020–3330 [2180]	431–4600 [2520]	2810–3630 [3220]	65–301 [183]	392–1070 [732]	347–904 [625]
Seed capsule	5	9.0–70 [27]	672–4160 [2410]	2700–5920 [4600]	563–1800 [1080]	38–305 [123]	191–1240 [738]	757–1390 [972]
Immature seeds	2	26–296 [161]	4340–4480 [4410]	6010–6090 [6050]	2740–7120 [4930]	70–661 [365]	3330–3880 [3610]	1940–3290 [2610]
Ripe seeds	1	85	9460	4570	4104	603	1856	2380
Young leaves	12	1.0–52 [20]	124–12200 [4100]	89–19500 [7250]	352–6900 [3020]	1.9–2320 [390]	34–5180 [1010]	152–3610 [1440]
Old leaves	21	12–69 [30]	2416–10900 [4730]	3101–13400 [5760]	1060–5500 [3140]	30–525 [120]	430–3220 [789]	1140–3100 [1660]
Bark	7	14–71 [43]	92–23405 [10870]	45–6239 [3750]	361–2160 [728]	19–530 [213]	16–505 [332]	108–1127 [749]
Phloem tissue	3	29–95 [51]	129–36400 [16500]	84–8420 [4970]	13–1360 [975]	26–384 [222]	30–339 [180]	152–1100 [735]
Twigs	14	1.0–71 [21]	130–25900 [5200]	246–13700 [5520]	109–5280 [966]	8.8–856 [313]	16–1730 [539]	53–1720 [610]
Wood	7	2.8–23 [14]	125–1296 [762]	78–2725 [1585]	85–249 [150]	5.0–483 [200]	23–791 [359]	48–506 [306]
Roots	1	91	125	53	382	31	40	81

All values provided in $\mu g\ g^{-1}$

Table 2-2. Elemental concentration (trace elements: Co, Cr, Cu, Fe, Mn, Ni, Zn) ranges and means in parentheses.

Plant part	*N* samples	Co	Cr	Cu	Fe	Mn	Ni	Zn
Flowers	2	16–104 [60]	14–17 [16]	6.5–9.5 [8.0]	15–24 [20]	34–945 [490]	2905–5560 [4230]	20–100 [60]
Seed capsule	5	4.3–31 [13]	2.3–17 [8.4]	2.2–10 [5.9]	8.0–30 [20]	11–83 [35]	1274–4001 [2660]	9.0–22 [17]
Immature seeds	2	23–89 [56]	15–28 [22]	8.5–13 [11]	30–43 [36]	58–64 [61]	754–1421 [1090]	26–34 [30]
Ripe seeds	1	3	114	14	131	187	17570	182
Young leaves	12	3.0–198 [46]	1.3–66 [16]	0.1–17 [6.7]	9–241 [63]	21–182 [93]	1105–10750 [5388]	10–244 [52]
Old leaves	21	12–75 [31]	1.2–13 [6.9]	0.9–11 [4.7]	22–90 [46]	95–461 [170]	11470–25060 [16490]	45–249 [85]
Bark	7	4.4–28 [14]	2.3–13 [6.3]	1.0–10 [4.5]	22–429 [85]	33–89 [66]	842–6820 [5260]	18–83 [69]
Phloem tissue	3	12–49 [27]	6.3–15 [10]	1.3–6.6 [4.1]	37–564 [220]	62–126 [103]	1390–9340 [5570]	28–191 [100]
Twigs	14	1.9–36 [16]	2.4–42 [8.0]	0.5–33 [6.2]	4.0–40 [17]	5.0–259 [72]	99–12300 [4330]	5.1–103 [49]
Wood	7	0.8–15 [5.0]	1.9–4.7 [3.4]	0.7–6.3 [2.5]	3.7–10 [5.7]	5.9–18 [11]	443–1170 [862]	4.8–14 [10]
Roots	1	26	6.5	0.7	512	164	1272	24

All values provided in µg g^{-1}

given in Table 2. Cobalt (Co) concentrations are the highest in the young leaves with up to 198 µg g^{-1}, but are comparatively low in relation to Ni concentrations. The mean Co:Ni quotient is 1:532, evidencing highly selective uptake of Ni over Co, compared to soil concentrations of these elements (generally 10:1 Ni to Co). Chromium (Cr) concentrations are universally low, and this element is clearly excluded from uptake. Copper (Cu) concentrations have a narrow range between 0.7–17 µg g^{-1}, with mean values of 6.7 and 4.7 µg g^{-1} in young and old leaves respectively. Iron concentrations are more variable, but generally low (maximum of 564 µg g^{-1} in the phloem tissue). Manganese (Mn) concentrations too are low in all plant parts, with the highest concentrations on the old leaves (up to 461 µg g^{-1}). Nickel concentrations are the highest in the old leaves with up to 2.50 Wt% (mean of 1.65 Wt%) and somewhat lower in the young leaves (up to 1.08 Wt% and a mean of 5390 µg g^{-1}). Nickel concentrations are also high in the twigs (up to 1.23 Wt%) and in the phloem tissue (up to 0.93 Wt%). It is remarkable that the reproductive organs (flowers, fruit capsule and seeds) are highly Ni-enriched. The seeds contain 1.76 Wt% Ni and the flowers on average 0.43 Wt% Ni. The elemental fractionation of Ni in the different plant parts is depicted in Fig. 2-5. Finally, zinc (Zn) concentrations are unremarkable with on average 85 µg g^{-1} in the old leaves.

Conservation status

The habitat of P. *rufuschaneyi* is outside any protected areas, in patches of remaining scrub in an area devastated by recurring forest fires. The restriction of this species to just one main population (the second population is very small) and the small area of occupancy (< 10 km2) means that this species is sensitive to disturbances which could ultimately lead to its extinction. Therefore, the species can be classified as Critically Endangered (CR) on the basis of IUCN Red List Criteria (Version 3.1: IUCN 2001) considering Criterion B. Geographic range; B2. Area of occupancy estimated to be less than 10 km2, and a. Severely fragmented or known to exist at only a single location; b. Continuing decline in (i) extent of occurrence; and (iii) area, extent and/or quality of habitat.

Discussion

The taxonomic position of *P. rufuschaneyi* is noteworthy as it represents the most western species of its subgenus. It is placed in *Phyllanthus* subgenus *Gomphidium* section *Nymania* (K.Schum) J.J.Sm. on account of its three paired staminate disc glands and its connate stamens (Fig. 2-3c). Section *Nymania* is mainly distributed in Papua New Guinea, but a few species also occur in the Philippines. *Phyllanthus rufuschaneyi* is most similar to *P. securinegioides*, however, it differs in its significantly smaller leaves, its smaller fascicled inflorescences with pinkish flowers (Fig. 2-1a; vs larger fascicles with yellow flowers *in P. securinegioides*), the completely fused anther filaments (Fig. 2-3c) and the fused style (Fig. 2-3e). The other Philippine species of *Gomphidium*, *P. apiculatus* Merr., *P. ramosii* Quisumb.,

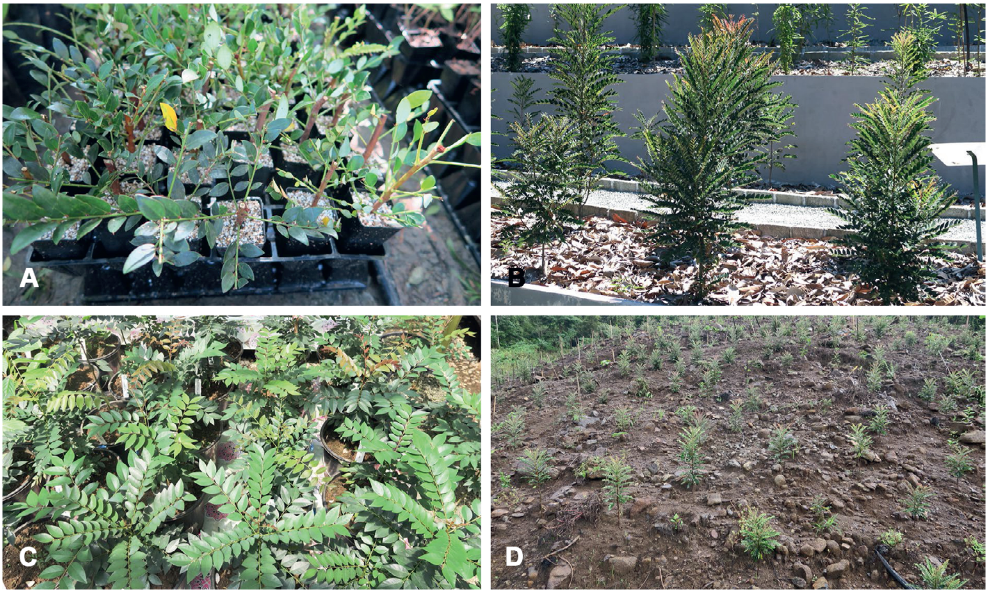

Figure 2-5. Agromining growth trials using *P. rufuschaneyi* in Sabah, Malaysia: A. Mass propagation of *P. rufuschaneyi* using cutting grown in perlite; B. *Phyllanthus rufuschaneyi* shrubs planted out in the 'Hyperaccumulator Botanic Garden' of Sabah Parks; C. plant nutrition growth experiment using *P. rufuschaneyi* at Monggis substation; D. full-scale (1.5 ha) agromining field trial using *P. rufuschaneyi* near Pahu village 6 months after planting.

P. glochidioides Elmer and *P. cordatulus* Rob., all have staminate flowers with free stamens. Though *P. cordatulus* has a similarly fused style of c. 1.3 mm long, it is spreading for about the same distance, whereas the style of *P. rufuschaneyi* is only fused for up to 1 mm and slightly erose at the end. The style is quite prominent and emerges out of the pistillate flowers (Fig. 2-3d, e). The other species of *Phyllanthus* occurring in Borneo are from other subgenera and differ either in their branching system (e.g. phyllanthoid vs non-phyllanthoid in subgenus *Macraea* (Wight) Jean F.Brunel) or in the morphology of their flowers (e.g. no difference between inner and outer sepals in subgenera *Emblica* (Gaertn.) Kurz, *Kirganelia* (A.Juss.) Kurz and *Eriococcus* (Hassk.) Croizat & Metcalf). The structure on top of the anther connective is slightly reminiscent of the apiculate anthers in subgenus *Phyllanthodendron* (Hemsl.) G.L.Webster. However, *P. rufuschaneyi* does not have the characteristic ligulate nectar disc and apiculate anthers that are also found in subgenus *Gomphidium*. Nickel hyperaccumulators are found in several subgenera within the genus *Phyllanthus*, which suggests that it evolved several times.

The restricted distribution of *P. rufuschaneyi* cannot be easily explained. In Sabah, Ni hyperaccumulators are restricted to circum-neutral soils with relatively high phytoavailable calcium, magnesium and Ni concentrations with at least 20 μg g^{-1} carboxylic acid extractable Ni or 630 μg g^{-1} total nickel, and a soil pH > 6.3 (Van der Ent et al. 2016b). However, these types of Cambisols derived from serpentinized bedrock are relatively widespread in Sabah, but *P. rufuschaneyi* has not been found elsewhere despite extensive fieldwork on all major ultramafic outcrops in Sabah (Van der Ent et al. 2015b). Although some Ni hyperaccumulators are comparatively common (*P. balgooyi*, *Psychotria sarmentosa* Blume, Rubiaceae, *Xylosma luzonensis*) on several ultramafic outcrops in Sabah, the situation of *P. rufuschaneyi* mirrors that of *Actephila alanbakeri*, which is also restricted to a single site at the same location (Van der Ent et al. 2016a). Experience in cultivation shows that *P. rufuschaneyi* is highly shade-intolerant and requires exposed conditions with minimal light competition (Fig. 2-5). It suffers from fungal infections when grown under shaded and moist conditions, and stops flowering. The dependence on a specific pollinator that is characteristic for the *Phyllanthus-Epicephala* mutualism and limited dispersal capabilities might be possible explanations why this species is not more widespread in Borneo. *Phyllanthus rufuschaneyi* has particularly attractive characteristics for cultivation as 'metal crop' in agromining operations. These favourable properties include its multi-stemmed habit, the rapid re-growth after coppicing, and high Ni concentrations in woody parts of the biomass. Other *Phyllanthus*-species, such as P. balgooyi, albeit having equally high foliar Ni concentrations, have lower growth rates and do not tolerate open and exposed conditions on bare soils. A major uncertainty currently pertains to the effective mass-propagation of *P. rufuschaneyi*, however, and the specialised pollination strategy of this species presents a challenge for using seed stock. More than any other species, obligate hyperaccumulator plants that have a restricted distribution on isolated ultramafic outcrops are susceptible to habitat degradation (Galey et al. 2017). *Phyllanthus rufuschaneyi* is known only from a site that has been severely affected by over-logging and (man-made) forest fires for clearing of agricultural land, and neither the area nor the species has statutory protection. The current expansion of oil palm plantations on Lompoyou Hill cast a further shadow over its continued existence in the wild. As such, the case of *P. rufuschaneyi* highlights the importance of habitat and germplasm preservation if rare species are to be used in green technologies such as agromining. Therefore, concerted efforts must be made to screen for hyperaccumulator species (Whiting et al. 2004), followed by appropriate methods for conserving them both in and ex situ (Erskine et al. 2012). The utilization of *P. rufuschaneyi* in agromining operations means that there are now likely to be more plants in cultivation than in the wild, and this will for now safeguard its future survival.

Authors' contributions

AvdE, PE and GE conducted the fieldwork and collected the plant specimens in Sabah. RB and PvW carried out the taxonomical study. AvdE undertook the laboratory analyses. All authors read and approved the final manuscript.

Acknowledgements
We thank Rimi Repin, Rositti Karim (Sabah Parks) and Postar Miun (Sabah Forestry Department) for their help during the fieldwork in Malaysia.

Ethics approval and consent to participate
The Sabah Biodiversity Council issued research permits for conducting research in Sabah, and Sabah Parks granted permission to conduct research in Kinabalu Park.

Funding
The French National Research Agency through the national "Investissements d' avenir" program (ANR-10-LABX-21, LABEX RESSOURCES21) and through the ANR-14-CE04-0005 Project "Agromine" is acknowledged for funding support to G. Echevarria and A. van der Ent. A. van der Ent is the recipient of a Discovery Early Career Researcher Award (DE160100429) from the Australian Research Council.

CHAPTER 3

Subgeneric delimitation of the plant genus *Phyllanthus* (Phyllanthaceae)

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Published in Blumea 63: 167 - 198. 2018

https://doi.org/10.3767/blumea.2018.63.02.14

Chapter 3

Subgeneric delimitation of the plant genus Phyllanthus (Phyllanthaceae)

Short title: Subgeneric delimitation of *Phyllanthus*

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Abstract

Over two centuries of taxonomic studies on the species rich genus *Phyllanthus* have culminated in a broad and complicated classification with many subgenera and (sub)sections. Past taxonomic work has only focused on local revisions, mostly because of the size of the genus. In this study we aim to summarize most of the taxonomic work in a list containing the infrageneric delimitations of *Phyllanthus*. This work will serve as a reference, placing most currently recognized species in subgenera and if possible, in sections for further study. Here we recognize 880 species of Phyllanthus, classified in 18 subgenera, 70 sections and 14 subsections. A few taxonomic changes are necessary to reconcile published phylogenetic data with the current classification. Subsections *Callidisci* and *Odontadenii* are raised to sectional rank, while section *Eleutherogynium* and section *Physoglochidion* are reduced to subsections and *P. oxycarpus* is transferred to the genus *Glochidion*. A provisional key for the subgeneric classification of *Phyllanthus* is provided.

Key words: infrageneric taxonomy, pantropical, paraphyletic, Phyllanthaceae, Phyllanthus

Introduction

With almost 900 species, the mostly pantropical *Phyllanthus* L. is the largest genus in the family Phyllanthaceae (Govaerts et al. 2000). When considering all vegetative and reproductive organs, *Phyllanthus* is one of the most diverse groups in the Angiosperms (Webster 1956). This diversity is exemplified by the multitude of subgenera and (sub)sections defined within the genus. In the past, most of these subgenera and some sections were treated at generic rank (Jussieu 1824, Baillon 1858), but were eventually all subsumed in a broad genus concept of *Phyllanthus* with numerous sections (Müller 1863, 1865, 1866). The last major changes to this concept at genus level have been the segregation of the genera *Glochidion* J.R.Forst. & G.Forst. (Kurz 1873) and *Margaritaria* L.f. (Webster 1957, 1979). The infrageneric structure of *Phyllanthus* was improved with the creation of several subgenera in a monographic work on the *Phyllanthus* species of the West Indies by Webster (1956, 1957, 1958). Subsequent revisionary work followed Webster's outline of subgenera and sections to illustrate the relations among groups within *Phyllanthus* (e.g. Bancilhon 1971; Webster & Airy Shaw 1971; Punt 1972; Airy Shaw 1975, 1980a; Brunel 1987; Rossignol et al. 1987; Santiago et al. 2006; Ralimanana & Hoffmann 2011, 2014; Ralimanana et al. 2013). Regional work on *Phyllanthus* (Merrill 1920, 1926; Pax & Hoffmann 1922; Beille 1925, 1927; Croizat 1942a, 1943b; Leandri 1958; Airy Shaw 1963, 1969, 1972, 1975, 1976, 1980a, 1980b, 1982; Webster 1986; Chantaranothai 2005; Silva & Sales 2006, 2008) and morphological studies (Punt 1967, 1972, 1973, 1980, 1986; Lobreau-Callen et al. 1988; Stuppy 1995; Chen et al. 2009; Jangid & Gupta 2016; Wu et al. 2016) extended the infrageneric groupings to create a working classification for most *Phyllanthus* species.

However, recent phylogenetic studies showed that several subgenera were polyphyletic and even *Phyllanthus* itself proved to be paraphyletic (Kathriarachchi et al. 2006). In the following taxonomic revisions some of the polyphyletic subgenera were divided in new monophyletic subgenera (Ralimanana & Hoffmann 2011, 2014a; Ralimanana *et al.* 2013), but discussion remained whether *Breynia* J.R.Forst. & G.Forst., *Glochidion* and *Sauropus* Blume should be subsumed into *Phyllanthus*. One solution is to subsume these genera in *Phyllanthus* to create a giant genus (Hoffmann et al. 2006, followed by Chakrabarty & Balakrishnan 2009b; Wagner & Lorence 2011; Kurosawa 2016) and the other is to split *Phyllanthus* into smaller, morphologically recognizable, monophyletic groups (Pruesapan et al. 2012; van Welzen et al. 2014a; Telford et al. 2016, followed by Chakrabarty & Balakrishnan 2012). A more exhaustive phylogenetic study with higher sampling presented the case to maintain *Breynia* (including *Sauropus*), *Synostemon* F.Muell. and *Glochidion* as monophyletic and morphologically recognizable genera (Pruesapan et al. 2008, 2012; van Welzen et al. 2014a), still leaving the rest of *Phyllanthus* in its current state, a paraphyletic genus. If *Phyllanthus* would be split, a larger phylogenetic study, which includes all subgenera and the majority of sections, is needed to prove which groups are monophyletic.

Phyllanthus is currently classified in about 18 subgenera with numerous sections by past revision work. The most notable revisions of *Phyllanthus* are those for the neotropics (Webster 2001b, 2002a, 2002b, 2004), Asia (Airy Shaw 1960, 1975, 1980, 1981; Webster & Airy Shaw 1971; Schmid 1991) and tropical Africa and Madagascar (Brunel 1987; Brunel & Roux 1975, 1976, 1977, 1981, 1984, 1985; Leandri 1958; Radcliffe-Smith 1974, 1996b; Ralimanana & Hoffmann 2011, 2014, Ralimanana et al. 2013). There is some discussion regarding the validity as publication of Brunel's thesis (1987). The thesis covers a large amount of work on the *Phyllanthus* species of Madagascar and Africa with many notes on subgenera and sections. Because it is a thesis, this work was treated as not validly published based on article 32 of the International Code of Botanical Nomenclature (McNeill et al. 2012) by Kathriarachchi et al. (2006). However, the thesis contains the name of a printing company and numbered copies have been distributed to several institutes, which is all in agreement with article 30.8, making it a validly published book. As such it is used in this publication. Several of the decisions in Brunel's thesis were accepted in recent revisions of *Phyllanthus* in Madagascar (Ralimanana & Hoffmann 2011, 2014, Ralimanana et al. 2013).

The checklist by Govaerts et al. (2000) is often used to estimate the number of species within *Phyllanthus,* but it does not contain an infrageneric division. An attempted synopsis of all the subgenera and sections was published by Kathriarachchi et al. (2006). However, only the species included in the phylogenetic study were mentioned and a complete taxonomic treatment of the genus is still wanting. We hope that this list may serve as a framework for future studies. If *Phyllanthus* should ever be split into various genera, this list can serve as a recommendation for the species to include.

Methods

In this study, we record 881 species, which are divided into 18 subgenera, 69 sections and 15 subsections (Appendix 3-1). Govaerts et al. (2000) recorded 833 species and the difference is mainly caused by the acceptance of Brunel (1987) and the addition of newly published species after their work. Based on a combination of morphological descriptions, classifications in literature and published phylogenetic work (e.g., Samuel et al. 2005; Kathriarachchi et al. 2006; Pruesapan et al. 2008, 2012; Manissorn et al. 2010; Challen et al. 2011; Luo et al. 2011a), we propose the current list for the subgeneric classification of *Phyllanthus*, in which we assign as many species as possible to subgenera and sections. Some placements are adopted from and are now validly published from Webster's unfinished manuscripts, which are available online (http://herbarium.ucdavis.edu/webster_manuscripts.html). For those species that were unplaced, we studied the distribution and morphological descriptions (mainly branching type and the morphology of the staminate flower), which allowed us to place them at least in subgenera. A synoptic key is provided by which most species can be placed in the appropriate subgenera and/or sections. However, sections and the species included have often not been the subject of recent taxonomic revisions or are based solely on palynological differences. This complicates the creation of a key that can accommodate all species of *Phyllanthus*. The most important literature is cited after each species, which either provides a direct placement or a morphological description. Hybrid species and infraspecific taxa were not included. Some combinations, partly required by changes in level, are published here, but only to solve nomenclatural anomalies (e.g., subsections that cannot be classified anymore in a section due to splitting of sections and changes in the taxonomic level of the taxa).

Taxonomy listing of *Phyllanthus*

We could assign 837 of the 880 species to a particular subgenus or (sub)section (Appendix 3-2), with some only listed as formerly in subgenus *Isocladus* or the synonymized section *Paraphyllanthus* Müll.Arg. One species of subgenus *Isocladus* G.L.Webster, *P. maderasatensis* L., was designated as the lectotype of the whole genus *Phyllanthus* by Ralimanana & Hoffmann (2011). However, *Phyllanthus niruri* L. was already designated as the lectotype of the genus *Phyllanthus* by Small (1913) and later independently confirmed by Webster (1956). Unfortunately, the remaining 43 species could not be assigned due to either incomplete descriptions, destroyed type specimens, or lack of collections. We have opted to place these species *incertae sedis* as their true relations need further detailed study.

The classification of several subgenera from Webster's original monographs (1956, 1957, 1958) has changed drastically. Subsequent palynological (e.g., Punt 1967, 1972, 1973, 1980, 1986; Lobreau-Callen et al. 1988) and phylogenetic studies (Kathriarachchi et al. 2006) have led to many new combinations and necessary transfers, some of which are discussed below.

Subgenus *Isocladus* Webster was created to include about 60 species with non-phyllanthoid branching (leaves on main stem not reduced to scales and lateral axes not deciduous) and consisted of originally four sections, *Loxopodium* G.L.Webster, *Anisolobium* Müll.Arg., *Macraea* (Wight) Baill. and *Paraphyllanthus* Müll.Arg. (Webster 1956). However, subsequent studies (Brunel 1987, Webster 2002b) have reduced the size of this subgenus considerably. The sections *Macraea* and *Ceramanthus* (Hassk.) Baill. (the latter with section *Anisolobium* merged with it; Punt 1972) were raised to subgeneric level by Brunel (1987). Section *Loxopodium* has been transferred to subgenus *Phyllanthus* on the basis of pollen characteristics and section *Paraphyllanthus* was placed in the synonymy of section *Isocladus* (Brunel 1987). Webster did create a new section in subgenus *Isocladus*, *Antipodanthus* G.L.Webster, which contained several neotropical and Australian species (Webster 2002a), but the Australian species appear to be better placed in section *Lysiandra* (F. Muell.) G.L.Webster of subgenus *Phyllanthus* (Bouman, unpublished data). Phylogenetic studies have confirmed the distinctness of subgenera *Macraea* and *Ceramanthus* from *Loxopodium* (Kathriararchchi et al. 2006). For section *Antipodanthus*, only one Australian species, *P. calycinus* Labill., and no neotropical species were included in the phylogeny by Kathriararchchi et al. (2006), in which the group appeared to be distinct from subgenus *Isocladus*. However, to elucidate the relationship between sections *Antipodanthus* and *Lysiandra* it is necessary to include more species in a phylogenetic study. Therefore section *Antipodanthus* is here maintained with no formal subgeneric placement.

Ralimanana & Hoffmann (2011) made the remainder of subgenus *Isocladus* (including former section *Paraphyllanthus*) monotypic, to only include *P. maderaspatensis* L., leaving some species unplaced and in need of revision.

All small shrubs and herbaceous *Phyllanthus* species were originally placed in subgenus *Phyllanthus*. The subgenus was shown to be polyphyletic (Kathriarachchi et al. 2006) and several subgenera are now recognized separately: subgenus *Swartziani* (G.L.Webster) Ralim. & Petra Hoffm., containing the neotropical herbaceous species of subsection *Swartziani*; subgenus *Afroswartziani* Ralim. & Petra Hoffm., comprising the palaeotropical species of former subsection *Swartziani* (largely comparable with section *Anthophyllus* Jean F.Brunel (Brunel 1987)), subgenus *Tenellanthus* Jean F.Brunel and subgenus *Phyllanthus.* Subgenus *Phyllanthus* now only contains sections *Almadenses* G.L.Webster, *Choretropsis* Müll. Arg., *Loxopodium* G.L.Webster, *Lysiandra*, *Phyllanthus* and *Salviniopsis* Holm-Niels. ex Jean F.Brunel. Section *Praephyllanthus* Jean F.Brunel was found to be closely related to the species of subgenus *Afroswartziani* (Kathriarachchi et al. 2006) and is transferred here to subgenus *Afroswartziani*. The type of section *Anthophyllus* was placed in subgenus *Swartziani*, but all other palaeotropical species, including subsections *Callidisci* Jean F.Brunel, *Fluitantoides* Jean F.Brunel and *Odontadenii* Jean F.Brunel & Roux (here raised to section level) are better placed in subgenus *Afroswartziani*. These two subgenera are closely related (see Kathriarachchi et al. 2006) and mostly distinguished by the inflorescences (unisexual in *Afroswartziani*, bisexual in *Swartziani*) (Ralimanana et al. 2013). The species in sections *Odontadenii, Fluitantoides* and *Callidisci* have unisexual inflorescences and are tentatively placed in subgenus *Afroswartziani*.

Subgenus *Kirganelia* (A.Juss.) Kurz is polyphyletic (Kathirarachchi et al. 2006) and currently consists of eight sections: *Anisonema* (A.Juss.) Griseb., *Brazzeani* Jean F.Brunel & Roux, *Chorisandra* (Wight) Müll.Arg., *Cicca* (L.) Müll. Arg., *Hemicicca* (Bail.) Müll.Arg., *Omphacodopsis* Jean F.Brunel, *Polyanthi* Jean F.Brunel and *Pseudomenarda* Müll.Arg. As noted by Ralimanana & Hoffmann (2011), the type species for subgenus *Kirganelia* is *P. casticum* P.Willemet, but *P. reticulatus* Poir. is the type species for the type section *Anisonema*. Some African and Madagascan species, originally attributed to this subgenus, were shown to be phylogenetically separate and placed in subgenus *Anesonemoides* (Jean F.Brunel) Ralim. & Petra Hoffm. (Ralimanana & Hoffmann 2014). Subgenus *Anesonemoides* differs from subgenus *Kirganelia* in fruit morphology (dehiscent in subgenus *Anesonemoides* versus baccate in subgenus *Kirganelia*), a lack of brachyblasts in some species of subgenus *Anesonemoides*, pollen with colpi bordered by parallel muri and the androecium (free or centrally fused stamens in subgenus *Anesonemoides* versus two sets of stamens (one fused, one free) in subgenus *Kirganelia*) (Ralimanana & Hoffmann 2014). Subgenus *Kirganelia* sections *Cicca* and *Chorisandra* were also shown to be in a clade separate from section *Anisonema* (Kathriarachchi et al. 2006), but no nomenclatural changes have yet been published.

The sections *Omphacodopsis*, *Polyanthi* and *Brazzeani* have not yet been included in any phylogenetic studies. Section *Brazzeani* was originally placed in subgenus *Conami* (Aubl.) G.L.Webster based on pollen characters (Brunel & Roux 1977), but these seem to have arisen through convergence and *Brazzeani* is better placed in subgenus *Kirganelia* (Meeuwis & Punt 1983). The stamen in the staminate flowers of section *Brazzeanii* are arranged in two sets, similarly to subgenus *Kirganelia* section *Anisonema*. Though still used in Kathriarachchi et al. (2006) and Ralimanana & Hoffmann (2011), section *Floribundi* Pax & K.Hoffm. was reorganized by Brunel (1987) into two new sections *Polyanthi* and *Omphacodopsis*, while the type species of section *Floribundi* (*P. muellerianus* (Kuntze) Exell) was transferred to section *Anisonema*, and the two sections were combined. Sections *Polyanthi* and *Omphacodopsis*, though distinguished by pollen and fruit (in)dehiscence by Brunel (1987), can possibly be combined (see Breteler 2012). The staminate flowers of these sections are similar to species in subgenus *Anesonemoides*, but the indehiscent fruit is more like subgenus *Kirganelia* section *Anisonema* or *Cicca*.

Subgenus *Emblica*, sections *Microglochidion* (Müll.Arg.) Müll.Arg., *Pityrocladus* G.L.Webster (subg. *Emblica*) and subgenus *Cyclanthera* G.L.Webster were not yet included in any phylogenetic research and their relationships within *Phyllanthus* are not well known. Webster chose to include section *Microglochidion* and *Pityrocladus* in the Asiatic subgenus *Emblica* on account of their similarity in pollen (Webster 2002b; Webster & Carpenter 2002, 2008). A possible relationship between subgenus *Cyclanthera* and subgenus *Xylophylla* was suggested by Brunel (1987), but not incorporated in the latest revision by Webster (2002b).

Kathriarachchi et al. (2006) listed several sections as "not assigned to subgenus", which are either already placed by other authors, placed here, or treated as synonyms. Sections *Bivia* Jean F.Brunel & Jacq.Roux, *Ceramanthus* (Hassk.) Baill. and *Cluytopsis* Müll.Arg. are all placed in subgenus *Ceramanthus* (Punt 1972; Brunel & Roux 1985; Brunel 1987). Section *Nymphanthus* (Lour.) Müll.Arg. has often been treated in subgenus *Phyllanthus* (Li 1987a), but is placed here in subgenus *Eriococcus* (Hassk.) Croizat & Metcalf based on its pollen morphology (see Webster 1958; Brunel 1987; Webster & Carpenter 2008). Species of subgenus *Eriococcus* occur in Asia and Australia and are characterized by the staminate flower with four sepals and two or four stamens. Section *Physoglochidion* Müll. Arg is placed here as a subsection under section *Gomphidium* Baill. based on the treatment of Schmid (1991), which is discussed below. Subgenus *Gomphidium* is a diverse group, with its main centres of diversity in New Guinea and New Caledonia. The monotypic section *Hemicicca* Baill. is here placed in subgenus *Kirganelia* based on its similarity in pollen (see Brunel 1987) and baccate fruits. The remaining previously un-assigned sections are here treated as synonyms: section *Heteroglochidion* Müll.Arg. is a synonym of subsection *Eleutherogynium* (Müll.Arg.) G.L.Webster ex R.W.Bouman (see below for new combination based on Webster 1986); sections *Meiandroglochidion* S.Moore and *Polyandroglochidion* S. Moore are synonyms of section *Adenoglochidion* (Müll.Arg.) Müll.Arg. (Schmid 1991); section *Pentaglochidion* Müll.Arg.is a homeotypic synonym of section *Leptonema* Baill. (see Baillon 1862b; Müller 1863). The type species of section *Hedycarpidium* Müll. Arg. has been re-identified as *Baccaurea javanica* (Blume) Müll.Arg (see Müll.Arg. 1866; Haegens 2000) and even though the name is sometimes still used (Thin 2007), it is invalid and the other species assigned to this section need to be re-evaluated. A small number of *Phyllanthus* species from Vietnam was placed in subgenus *Eriococcus* subsection *Integra* Thin (see Thin 2007), which is not included in our list. No description was provided and it is quite possibly a synonym of subgenus *Eriococcus* subsection *Spiciferens* Jean F.Brunel as they include some of the same species, but we were not able to see the original publication.

Some nomenclatural issues are still present within *Phyllanthus*, particularly when looking at the names of subdivisions of certain subgenera. Recommendation 22A of the International Code of Nomenclature (McNeill et al. 2012) states that if there are no problems any subdivision of a subgenus that bears the type, should be given the same epithet. However in a few subgenera, this is currently not the case (Webster 1960). The type section of subgenus *Conami* is section *Nothoclema* G.L.Webster and the type section of subgenus *Kirganelia* is *Anisonema*. In subgenus *Kirganelia* section *Cicca*, the type species, *P. acidus* (L.) Skeels, is in subsection *Cheramela* Kuntze (Webster 2001b).

Taxonomic changes

Phyllanthus subgenus **Afroswartziani** Ralim. & Petra Hoffm. section **Callidisci** (Jean F.Brunel) R.W.Bouman, stat nov.—*Phyllanthus* subsect. *Callidisci* Jean F.Brunel, Gen. *Phyllanthus* Afr. Intertrop. Madag. (1987) 334. — Type: *Phyllanthus callidiscus* Jean F.Brunel

Note — Species of section *Callidisci* were originally placed by Brunel (1987) in subgenus *Phyllanthus* section *Anthophyllus* together with other palaeotropical subsections and recognized by the fringed disc in the pistillate flowers. As this group has recently been shown to be polyphyletic (Kathriarachchi et al. 2006) and after revision were split into a few new subgenera (Ralimanana et al. 2013), it seems necessary also to transfer Brunel's subsections. All other palaeotropical species of subgenus *Phyllanthus* were placed in subgenus *Afroswartziani* and were distinguished from the neotropical subgenus *Swartziani* by their unisexual inflorescences (Ralimanana et al. 2013). This is in agreement with species of subsection *Callidisci*, which is transferred here and raised to sectional level to accommodate the separation from section *Anthophyllus*.

Phyllanthus subgenus **Afroswartziani** Ralim. & Petra Hoffm. section **Odontadenii** (Jean F.Brunel & Jacq.Roux) R.W.Bouman, stat nov.—*Phyllanthus* subsect. Odontadenii Jean F.Brunel & Jacq.Roux, Willdenowia 11 (1981) 70; Brunel, Gen. *Phyllanthus* Afr. Intertrop. Madag. (1987) 339. — Type: *Phyllanthus odontadensis*

Müll.Arg.
Note — Species in the palaeotropical section *Odontadenii* also have unisexual inflorescences and are therefore more suited to be placed in subgenus *Afroswartziani* then the neotropical subgenus *Swartziani*. The species are distingusihed form other sections by their winged plagiotropic branchlets (Brunel & Roux 1981).

Phyllanthus subgenus **Gomphidium** (Baill.) G.L.Webster section **Adenoglochidion** (Müll.Arg.) Müll.Arg. subsection **Eleutherogynium** (Müll.Arg.) G.L.Webster ex R.W.Bouman, stat nov. — *Phyllanthus* sect. *Eleutherogynium* Müll. Arg., Linnaea 32 (1863) 4, 14. — Type: *Phyllanthus loranthoides* Baill.
Glochidion sect. *Chorizogynium* Müll.Arg., Linnaea 32 (1863) 58, 59. — Lectotype (designated by Webster 1986): *Phyllanthus macrochorion* Baill.
Phyllanthus sect. *Heteroglochidion* Müll.Arg. in A.DC., Prodr. 15,2 (1866) 319. — Type: *Phyllanthus baladensis* Baill.
Phyllanthus sect. *Scleroglochidion* Müll.Arg. in A.DC., Prodr. 15,2 (1866) 317. — Type: *Phyllanthus myrianthus* Müll.Arg.
Note — Section *Scleroglochidion*. was previously placed in synonymy by Webster (1986) who expanded the description of *Eleuterhogynium* to include also *Phyllanthus* species with 3 free filaments. Section *Heteroglochidion* was defined by Müller on its biseriate sepals, which is a common character for subgenus *Gomphidium*. All of these sections are characterized by a rudimentary to absent nectar disc (see Müll.Arg. 1866). Lobreau-Callen et al. (1988) in a palynological study, showed that the pollen of these groups showed a continuous variation in pollen characters and were difficult to differentiate. The lack of distinguishing floral and vegetative characters and the overlap in palynological characters leads us to the decision to combine the above sections in one subsection *Eleutherogynium*, with as main character the absent nectar disc to distinguish it from other species within section *Adenoglochidion*.

Phyllanthus subgenus **Gomphidium** (Baill.) G.L.Webster section **Gomphidium Baill.** subsection **Physoglochidion** (Müll.Arg.) R.W.Bouman, stat nov.— *Glochidion* sect. *Physoglochidion* Müll.Arg., Linnaea 32 (1863) 58.— *Phyllanthus* sect. *Physoglochidion* (Müll.Arg.) Müll.Arg., Prodr. 15,2 (1866) 318. — Type: *Phyllanthus faguetii* Baill.
Phyllanthus sect. *Phyllocalyx* Baill., Adansonia 2 (1862b) 236 (nom. illeg., non *Phyllocalyx* A.Richert, 1847)— *Glochidion* sect. *Physoglochidion* Müll.Arg., Linnaea 32 (1863) 58, 71. — Lectotype (designated here by R.W.Bouman, but see Webster (2001) manuscript synopsis of *Gomphidium*): *Phyllanthus faguetii* Baill.
Note — *Phyllanthus* section *Physoglochidion* (Müll.Arg.) Müll.Arg. is characterized by 3 free stamens, 6 sepals in two whorls and a calyx that becomes saccate in fruit. Apart from the saccate calyx, these characters also occur in section *Gomphidium*

and within section *Physoglochidion* and the saccate calyx shows a continuous variation between species (Lobreau-Callen et al. 1988). Since these groups can also not be distinguished on palynological data we opt to reduce section *Physoglochidion* to a subsection level and place it with section *Gomphidium*.

Transfer of *Phyllanthus oxycarpus* to *Glochidion*:
Glochidion oxycarpum (Müll.Arg.) R.W.Bouman, comb. nov.
Phyllanthus oxycarpus Müll.Arg., Prodr. 15,2 (1866) 1270. – *Diasperus oxycarpus* (Müll.Arg.) Kuntze, Rev. Gen. Pl. 2 (1891) 600. – Type: *Teijsmann* s.n. (holotype GDC), Indonesia, Sumatra.
Note — In his treatment of the genus *Phyllanthus* for de Candolle, Müller (1866) reduced the genus *Glochidion* to a few sections within *Phyllanthus*. *Phyllanthus oxycarpus* Müll.Arg. was first described by Müller (1866) and placed in section *Euglochidion* Müll.Arg. as it closely resembled *P. subscandens* (Zoll. & Moritzi) Müll. Arg. (a synonym of *G. zeylanicum* (Gaertn.) A.Juss.). Other species first published in section *Euglochidion* by Müll.Arg. were all transferred to the genus by other authors (e.g., Boerlage 1900; Koorders & Valeton 1910), but we were unable to find a transfer for *G. oxycarpum*. The description lists no nectar disc, a 5-6-locular ovary with columnar style, which are all typical features for the genus *Glochidion* and therefore this species is transferred here.

Key to the subgenera and (sub) sections of *Phyllanthus*

A provisional key is here provided based on characters mentioned in the literature. A key for full identification purposes, using morphology only (not pollen) is difficult due to the absence of recent complete treatments for several groups and the fact that some characters have evolved multiple times within *Phyllanthus*. The key is not completely dichotomous (trichotomous questions are marked with *) Authors of the various subgenera, sections and subsections are listed in Appendix 3-1 and all species within a particular group are listed in Appendix 3-2.

1. Branching non-phyllanthoid (laminate leaves and flowers on all axes, branchlets not deciduous)..2
1. Branching phyllanthoid (leaves on main stem reduced to scales, cataphylls, laminate leaves and flowers on lateral axes, lateral branchlets deciduous) or sub-phyllanthoid (leaves at base of branchlets not reduced to scales (often in juveniles), lateral branchlets deciduous).. 15

2. Aquatic herbs............... Subgenus *Phyllanthus* section *Salviniopsis* (Americas)
2. Herbs, shrubs or trees, but not aquatic 3

3. Palm-like (monocaul) shrubs to trees; stigma petaloid ....Subgenus *Xylophylla* section *Asterandra* (South America)

3. Herbs, shrubs to small trees, rarely climbers; stigmas variously bifid to multifid, not petaloid 4

4. Leaves on all axes spirally arranged 5
4. Leaves on all axes distichous 9

5. Sepals 4 in staminate flowers, 6 in pistillate flowers; staminate disc entire, H-shaped around filaments; stamens 2, filaments free .... Subgenus *Swartziani* section *Reverchonia* (North America)
5. Sepals 5–6 sepals in both sexes; staminate disc segmented; stamens 3 or 5, filaments free or connate 6

6. Sepals 5; stamens 5, filaments free .... Subgenus *Kirganelia* section *Pseudomenarda* (Africa)
6. Sepals 5–6 sepals; stamens usually 3, filaments connate (free in *P. rosmarinifolius* Müll.Arg.) 7

7. Inflorescences axillary cymules with 1–4 flowers; pistillate disc consisting of free glands .... Subgenus *Isocladus* (Africa and Asia, introduced in North America)
7. Inflorescences axillary cymules or thyrses; pistillate disc entire 8

8. Inflorescences axillary glomerules; pollen 3–4-colporate, subglobose .... Section *Antipodanthus* incertae sedis (South America & Australia?)
8. Inflorescences axillary glomerules or thyrses (sometimes paniculate at end of branch); pollen areolate .... Subgenus *Xylophylla* section *Elutanthos* (Central and South America)

9. Staminate disc segmented, pistillate disc entire or segmented; filaments free 10
9. Staminate disc segmented, or entire and urceolate, pistillate disc often massive and urceolate; filaments connate — pollen with macroreticulate exine .... 12 (subgenus *Ceramanthus*)

10. Anthers dehiscing with horizontal slits; pollen 4-colporate .... Subgenus *Phyllanthus* section *Loxopodium* (Americas)
10. Anthers often deflexed, but dehiscing with vertical slits; pollen clypeate or perisyncolporate 11

11. Leaves distichous; pollen clypeate; seeds verrucate or smooth .... Subgenus *Macraea* (Africa, Asia, Australia and Pacific)
11. Leaves spiral at basal nodes, distichous at upper nodes; pollen grains

perisyncolporate with median pores, colpi bordered by parallel muri; seeds smooth or striate .... Subgenus *Betsileani* (Madagascar)

12. Staminate flowers with sepals 4 (6 in pistillate ones); staminate disc consisting of 4 massive segments; stamens 2, filaments connate and thecae on an enlarged connective — pollen stephanoporate .... Subgenus *Ceramanthus* section *Bivia* (Africa)
12. Sepals 6 in both sexes; staminate disc entire or 6 segments; stamens 3 with connate filaments, thecae not on an enlarged connective 13

13. Staminate disc entire and cup-shaped.. .... Subgenus *Ceramanthus* section *Ceramanthus* (Asia)
13. Staminate disc segmented or only slightly fused into a ring 14

14. Sepals in two dimorphic whorls; staminate disc segmented; pollen peribrevicolporate .... Subgenus *Ceramanthus* section *Anisolobium* (Africa and Asia)
14. Sepals in two equal whorls; staminate disc segmented to slightly fused into a ring; pollen pantoporate......Subgenus *Ceramanthus* section *Cluytopsis* (Asia)

15. Branching sub-phyllanthoid 16
15. Branching phyllanthoid (sometimes sub-phyllanthoid in very young plants, check mature plants)... 20

16. Branchlets short, with only 5–10 leaves (Webster 2001b); staminate disc entire .... Subgenus *Xylophylla* section *Brachycladus* (South America and Central America)
16. Branchlet length variable, usually bearing more than 10 leaves; staminate disc segmented 17

17. Anther connective not enlarged; fruit an indehiscent capsule; seeds smooth with fleshy sarcotesta ....Subgenus *Conami* section *Hylaeanthus* (South America and West Indies)
17. Anther connective variable, often enlarged; fruit a dehiscent capsule; seeds ornamented, without a fleshy sarcotesta 18

18. Filaments connate, stamens mostly 3 ....26 (subgenus *Afroswartziani*)
18. Filaments free (filaments connate in *P. allemii* G.L.Webster and *P. fastigiatus* Mart ex Müll.Arg., but then only 2 stamens) 19

19. Anther connective often enlarged, thecae not appearing as stipitate; seeds

scalariform with slight transverse striations or smooth.......................................
.Subgenus *Phyllanthus* section *Lysiandra* (Australia and Central America(?))

19. Anther connective variable, sometimes deeply emarginate with the two thecae appearing to be stipitate; seeds striate or linearly verrucate....................
.....Subgenus *Phyllanthus* section *Phyllanthus* subsection *Clausseniani* (South America)

20. Herbs or subshrubs.. 21
20. Shrubs to trees, rarely climbers 36

21. Herbs; each branchlet bearing just one pair of (sub)opposite leaves and terminating in a raceme; anther connective enlarged...
......Subgenus *Phyllanthus* section *Phyllanthus* subsection *Almadanses* (South America)
21. Herbs or subshrubs; branchlet with more than 2 alternate leaves and flowers in leaf axils; anther connective (not) enlarged 22

22. Flowers 5-merous; stamens 5, filaments free (except 3 stamens in *P. cocumbiensis* Jean F.Brunel) — pollen subglobose, 3-4-colporate ....
................................23 (Subgenus *Tenellanthus* pantropical, but origin Africa)
22. Flowers 5-6-merous; stamens 2–3, filaments free or connate........................ 24

23*. Shrubs or hemicryptophytes; stamens 5, filaments basally united; pollen 3-colporate, with macroreticulate exine. Seeds with fine punctuation..............
.... Subgenus *Tenellanthus* section *Loandani* (Africa)
23*. Herbs; stamens 5 (3 in *P. cocumbiensis*), filaments connate or free; pollen 3-colporate, with tectate, microperforate exine ....
....Subgenus *Tenellanthus* section *Pentandra*(Africa)
23*. Herbs or subshrubs; stamens 5, filaments completely free; pollen 4-colporate with sponge-like exine..
..Subgenus *Tenellanthus* section *Tenellanthus* (pantropical, but origin Africa)

24. Inflorescences unisexual.. 25
24. Inflorescences bisexual.. 35

25. Cataphyllary stipules (unilaterally) auriculate 26
25. Cataphyllary stipules not auriculate 32

26. Leaf base symmetric; plagiotropic branches carinate (winged) (Brunel & Roux 1981). Pollen exine tectate; seeds with longitudinal striae or smooth.....
.... Subgenus *Afroswartziani* section *Odontadenii* (Africa)
26. Leaf base asymmetric; plagiotropic branches not carinate............................. 27

27. Pistillate disc entire with delicate fringes...Subgenus *Afroswartziani* section *Callidisci* (Africa)
27. Pistillate disc entire, but not fringed... 28

28. Sepals 5 in staminate flowers.. 29
28. Sepals 6 in staminate flowers.. 30

29. Cataphyllary stipules usually black and indurate; stamen 2–3, filaments partially or wholly connate, anthers sometimes deeply emarginate, dehiscing mostly horizontal; seeds longitudinally striate or banded, possibly with transverse striae. Pollen 3-colporate.. ...... Subgenus *Phyllanthus* section *Phyllanthus* subsection *Pentaphyllus* (West Indies)
29. Cataphyllary stipules thin and membranous, not indurate or black; stamen 3, filaments connate, anthers not emarginate, dehiscing horizontally to vertically; seeds longitudinally striate 30

30. Pistillate inflorescences on proximal position and staminate inflorescences on distal position of plagiotropic branchlets; seeds transversely striate — ovary often covered with tubercles... .... Subgenus *Emblica* section *Urinaria* (pantropical, but origin Asia)
30. Pistillate inflorescences on distal position and staminate inflorescences on proximal position of plagiotropic branchlets; seeds longitudinally striate .. 31 (Subgenus *Afroswartziani*)

31*. Pollen 3–4-colporate, exine bireticulate........Subgenus *Afroswartziani* section *Praephyllanthus* (Africa)
31*. Pollen 3-sulcate, exine macroreticulate. Often found in water......................... ....Subgenus *Afroswartziani* section *Fluitantoides* (Africa)
31*. Pollen perihexabrevisulcate, exine macro-rugulose (Brunel 1987). Ovary on gynophore .... Subgenus *Afroswartziani* section *Microdendron* (Africa)

32. Branchlets and flowers not purplish; stamens 3, filaments mostly free or united to 2/3 of length; pollen 4-colporate, exine (hetero-)reticulate; pistillate sepals 5; pistillate disc entire; stigmas free, bifid, tips sometimes subcapitate33
32. Branchlets and flowers often purplish; stamens 2 or 3, filaments connate; pollen pantoporate, exine shields elongated or if round with only 1 pila; pistillate sepals 6; pistillate disc dissected or lobed; stigmas free or connate, bifid to emarginate, tips not capitate .... 34 (Subgenus *Cyclanthera*)

33. Anther connective not enlarged, thecae not stipitate; style branches sub-

capitate; seeds verrucate .... Subgenus *Phyllanthus* section *Phyllanthus* subsection *Niruri* (South America, pantropically invasive)

33. Anther connective variable, deeply emarginate with the two thecae appearing stipitate; style branches not capitate; seeds striate or linearly verrucate ....Subgenus *Phyllanthus* section *Phyllanthus* subsection *Clausseniani* (South America)

34. Branchlets unramified, rooting at nodes; leaves crisply succulent; stamens 2, filaments free; pollen shields elongated (banded) (Webster & Carpenter 2002) ....Subgenus *Cyclanthera* section *Callitrichoides* (West Indies)

34. Branchlets often with 1 or 2 lateral branches (bipinnatiform), not rooting at nodes; leaves not succulent; stamens 3, filaments completely connate into a circular synandrium; pollen shields isodiametric, each with a central pila surrounded by a murus (Webster & Carpenter 2002) .... Subgenus *Cyclanthera* section *Cylcanthera* (West Indies)

35. Stamens 3, filaments free, anthers dehiscing horizontally; pistillate disc dissected; pollen grains brevicolporate and diorate or porate, exine pilate; seeds verruculose .... Subgenus *Conami* section *Apolepsis* (South America)

35. Stamens 2 or 3, filaments entirely or partially connate (free in *P. warnockii* G.L.Webster), anthers dehiscing oblique to horizontally (vertically in *P. warnockii*); pistillate disc entire; pollen 3-colporate, exine reticulate; seeds smooth or longitudinally striate........... Subgenus *Swartziani* (North America, pantropical invasive)

36. Leaves reduced and branchlets transformed to phylloclades (at least in older branches) 37

36. Leaves not reduced and branchlets not transformed to phylloclades........... 39

37. All stems rounded or flat; stipules unilaterally auriculate, stamens free or connate; pollen 3–4-colporate, exine reticulate ....38 (Subgenus *Phyllanthus* section *Choretropsis*)

37. Lateral stems flattened with wide phylloclades, (bi-)pinnatiform; stipules not auriculate; stamens usually united at base; pollen clypeate, exine areolate... Subgenus *Xylophylla* section *Xylophylla* (West Indies)

38. Main axes often flat, branching monopodial, leaves distichous; inflorescences usually bisexual, stamens 3 (rarely 4)................. Subgenus *Phyllanthus* section *Choretropsis* subsection *Applanata* (South America)

38. Main axes rounded, branching monopodial or sympodial, leaves spiral; inflorescences mostly unisexual; stamens 2 or 3...

....Subgenus *Phyllanthus* section *Choretropsi*s subsection *Choretropsis* (South America)

39. Fruits indehiscent, berries or drupes... 40
39. Fruits dehiscent, capsules (or absent).. 48

40. Fruits drupaceous.. 41
40. Fruits baccate.. 43

41. Sepals 6; stamens 3, filaments connate.......Subgenus *Emblica* section *Emblica* (Asia)
41. Sepals 4–6; stamens 3–4(rarely 2 or 5), filaments free .... 42 (Subgenus *Kirganelia* section *Cicca*)

42. Plants dioecious; disc absent in both sexes; staminodes absent; fruits spongy (Webster 1957) .... Subgenus *Kirganelia* section *Cicca* subsection *Aporosella* (West Indies and South America)
42. Plants monoecious; disc present in both sexes; sometimes staminodes present; fruits hard... ....Subgenus *Kirganelia* section *Cicca* subsection *Cheramella* (commonly cultivated, origin possibly African?)

43. Stamen 2, filaments connate; ovary 2-locular ....Subgenus *Kirganelia* section *Chorisandra* (Africa, Madagascar, Mainland Asia)
43. Stamen 3-6, filaments free or connate; ovary 3-locular................................. 44

44. Branchlets subtended by reduced leaves, but not cataphylls, flowers on brachyblasts; stamens 3, filaments free or connate... ....Subgenus *Conami* section *Hylaeanthus* (South America)
44. Branchlets subtended by (spinescent) cataphylls, stamens 4-6, filaments free. 45

45. Branchlets subtended by spinescent cataphylls; stamens 5 in 2 sets, one free and the other basally fused ....Subgenus *Kirganelia* section *Anisonema* (Africa and Asia)
45. Branchlets subtended by scale or stipule like cataphylls; stamens 4–6, filaments free 46

46. Staminate inflorescences on separate (leafless) plagiotropic branches, pistillate flowers axillary — seeds globular, smooth......... Subgenus *Kirganelia*

section *Polyanthi* (Africa)
46. Inflorescences axillary, on all plagiotropic branches 47

47. Stamens 5 .... Subgenus *Kirganelia* section *Hemicicca* (Asia)
47. Stamens 6 ...... Subgenus *Kirganelia* section *Chorisandra* (Africa, Madagascar, Mainland Asia)

48. Anthers apiculate... 49
48. Anthers non-apiculate 56

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78*. Inflorescences glomerules; pollen diverse, often 3-colporate with diorate

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101. Brachyblasts often present; sepals 5; staminate disc consisting of 5 segments; stamens 3 (rarely 4); fruit a large fleshy capsule (usually >2 cm in diameter).. ....Subgenus *Xylophylla* section *Omphacodes* (West Indies)
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vertically; style like an erect tube, stigma branches narrowed to acute tips...... Subgenus *Xylophylla* section *Thamnocharis* (West Indies)

Discussion & Conclusion

Taxonomic discussions on the circumscription of genus *Phyllanthus* are still ongoing, mainly with the question whether the genera nested within should be subsumed (Hoffmann et al. 2006) or remain separate (van Welzen et al. 2014a). However, a good understanding and clear structure within the genus *Phyllanthus* in its current circumscription is necessary. Here an attempt was made to summarize over 200 years of taxonomic work on this immense group. Several issues that still exist will hopefully be resolved in new systematic studies. The provisional key to the subgenera and (sub) sections provided here works with most typical examples of *Phyllanthus* species. Future research and revision work should focus on treatments of the individual subgenera and/or sections within the genus.

Unfortunately not all species could be fitted in this subgeneric classification due to exceptional characters or incomplete descriptions (see Appendix 3-2). These will need further study or more new collections to elucidate their place within the genus. Often these are species of which only the type specimen is known and which were not collected since, and some might be extinct (e.g., *P. aoraiensis* Nadeaud; Wagner & Lorence 2011), or they might be exceptional forms, which should be united with other species. For some we could only assign them to subgenus level and further revision work should place them in their appropriate sections. The placement of some species may change with new research and we welcome these changes as they will lead to a better understanding of the genus *Phyllanthus* and we hope this article inspires discussion.

Several issues are still unresolved and will require further attention. Subgenus *Phyllanthus*, which previously spanned all herbaceous species, remains difficult and more species need to be included in new phylogenetic studies. Several groups in our list have not had formal taxonomic treatment for some time and new revision work may identify new species and better characters to differentiate them within *Phyllanthus*. Another taxonomic problem was created by the discussions on the validity of Brunel's thesis (1987), which has led to many species being published twice under different names (see Radcliffe-Smith 1996b). This will require close scrutiny in determining how many should be synonymized. Finally, a decision should be made on how to treat the paraphyly of the genus *Phyllanthus*. Whether the genus will be split or whether the clades will be subsumed within *Phyllanthus*, we hope that this treatment will provide structure to this diverse genus.

Acknowledgements

This work was done as part of the PhD research of the main author, funded by the Hortus botanicus Leiden and Leiden University. Help with preparing the list for the manuscript by Peter Hovenkamp is gratefully acknowledged. The second author thanks the Leiden University Fund (LUF) for their support of the chair Botanical gardens and botany of Southeast Asia. The last author thanks the Treub Maatschappij, the Society for the Advancement of Research in the Tropics, for their support of the Ornstein chair in Tropical Plant Biogeography.

Appendix 3-1. Synopsis of the infrageneric classification of the genus *Phyllanthus*. Author of type species can be found in Appendix 3-2. Countries in parentheses indicate unlikely disjunct ditributions that require further study. Available at: https://doi.org/10.3767/blumea.2018.63.02.14

Appendix 3-2. Species checklist of *Phyllanthus* based on the current infrageneric classification. Each species denotation contains information on whether the classification was based on morphology, literature references or phylogenetic evidence. Unsure placements are noted with 'loc' for location based placements, a question mark and/or a ~ symbol when morphology does not completely comply with the group. Available at:
https://doi.org/10.3767/blumea.2018.63.02.14

CHAPTER 4

A taxonomic revision of *Phyllanthus* subgenus *Macraea* (Phyllanthaceae)

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Published in Blumea 64: 231 - 252. 2019

https://doi.org/10.3767/blumea.2019.64.03.05

Chapter 4

A taxonomic revision of *Phyllanthus* subgenus *Macraea* (*Phyllanthaceae*)

Short title: Taxonomic revision of *Phyllanthus* subgenus *Macraea*

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Abstract

Within the morphologically diverse pantropical genus *Phyllanthus*, many subgenera, sections and subsections are recognized. While most taxonomic revisions often focus on local floras, closely related and often resembling species are not always treated in full. Subgenus *Macraea* is here revised for the first time over its whole distribution, including an identification key and descriptions of its species with distributions, ecology, uses and vernacular names. The currently acknowledged varieties of *Phyllanthus distichus* are rejected due to inadequate morphological differences. *Phyllanthus panayensis* is synonymized with *P. lancifolius*. *Phyllanthus alpestris* has now become a variety of *P. glaucophyllus* because of the resemblance in morphology and distribution. The species complex around *Phyllanthus virgatus* remains taxonomically difficult, but *Phyllanthus virgatus* var. *gardnerianus* and *Phyllanthus virgatus* var. *hirtellus* are here recognized on the species level as *P. gardnerianus*, *stat nov.* and *P. tararae*, *stat & nom nov.* A new species from the Philippines, *Phyllanthus ridsdalei*, is described.

Keywords: *Euphorbiaceae*, *Macraea*, new species, *Phyllanthaceae*, *Phyllanthus*, revision, species descriptions, taxonomy.

Introduction

Phyllanthus L. is the largest genus in the family *Phyllanthaceae* (Kathriarachchi et al. 2006), and occurs in the tropics and subtropics of all continents (Ralimanana & Hoffmann 2011). The genus displays a large morphological variety, both in habit and floral characters (Webster 1956; Ralimanana & Hoffmann 2011). As a result of this large morphological variety within the over 800 species recorded for Phyllanthus, the classification of the species is challenging (Webster 1956; Govaerts et al. 2000; Kathriarachchi et al. 2006). Currently, due to its size, morphological variability and history, *Phyllanthus* is divided into a considerable number of subgenera, sections and subsections (Bouman et al. under review). *Phyllanthus* is paraphyletic (Wurdack et al. 2004; Kathriarachchi et al. 2006; Pruesapan et al. 2008), which could be solved by subsuming the presently recognized genera *Breynia* J.R.Forst. & G.Forst., *Synostemon* F.Muell. and *Glochidion* J.R.Forst. & G.Forst. (van Welzen et al. 2014a) into *Phyllanthus* and creating a large monophylectic genus (Kathriarachchi et al. 2006; Hoffmann et al. 2006; Webster 2007; Kurosawa 2016). However, this is not preferred by some authors (Pruesapan et al. 2008; 2012; van Welzen et al. 2014a; Barrett & Telford 2015), because this only moves the problem to infrageneric ranks and makes *Phyllanthus* a giant, unrecognizable and unmanageable genus. The alternative is to split *Phyllanthus* into smaller monophyletic genera, for example by using the monophyletic clades found by Kathriarachchi et al. (2006) and Pruesapan et al. (2008; 2012), when these are morphologically recognizable. *Phyllanthus* subgenus *Macraea* (Wight) Jean F.Brunel is one of these monophyletic clades (Kathriarachchi et al. 2006), which may be considered for recognition on the genus level.

Wight (1852) described *Macraea* as a separate genus, but noted that it was not very distinct from *Phyllanthus*, the principal difference being the free stamens of *Macraea*, as opposed to the united ones of known *Phyllanthus* species. He named the genus after a synonymized orchid genus with the same name from the botanist Lindley (Wight 1852). Because Wight did not designate a type, Webster (1986) chose *Macraea oblongifolia* Wight as the lectotype of the subgenus. This species had already been synonymized under *Phyllanthus simplex* Retz. by Müller (1866) and is currently recognized as a synonym of *Phyllanthus virgatus* G.Forst. (Govaerts et al. 2000). Brunel (1987) gave *Macraea* its current rank of subgenus and included two sections: *Macraea* sect. *Macraea* and sect. *Praemacraea* Jean F.Brunel. The latter was shown to be phylogenetically distinct and raised to subgenus *Betsileani* (Jean F.Brunel) Ralim. & Petra Hoffm. (Kathriarachchi et al. 2006; Ralimanana & Hoffmann 2011). There is some discussion about the legitimacy of the publication of the PhD thesis of Brunel (1987) in which he published these changes. According to ICN (Turland et al. 2018) article 30.9 the thesis can be and is accepted by us as a validly published book, since it contains the name of a printing company, is distributed to several institutes and has been written with all considerations of the code taken into account. In this treatment, we follow Brunel's definition of subgenus *Macraea* as separate from subgenus *Isocladus*, but with the exclusion of (former) section *Praemacraea*.

Subgenus *Macraea* occurs only in the palaeotropics (Webster 1986) and small centres of diversity can be found in Sri Lanka, the Philippines, Australia and various islands in the Pacific. It is a clade of monoecious (rarely dioecious) herbs, (sub) shrubs and trees, characterised by non-phyllanthoid branching; a 6-parted perianth (but often 4-parted in one species); a dissected staminate disc; 3 stamens (but often 2 in one species), free filaments (but variably connate in some species); spherical, clypeate pollen grains (Webster 1986; Brunel 1987; Punt 1980; Chen et al. 2009; Wu et al. 2016); smooth or verrucate seeds; triangular or ovate, translucent, chestnut-brown stipules with often an auriculate base and laminate stem leaves. The leaves are distichous on all axes. Previous studies have shown that pollen characteristics are especially useful in differentiating between clades within *Phyllanthus* (Webster 1956; Punt 1967, 1972; Wu et al. 2016), and as such can be used for distinguising *Macraea* species from other *Phyllanthus* species. A few Philippine and Pacific species are here transferred to subgenus *Macraea* based on previous palynological studies (e.g., *P. lancifolius* Merr., *P. pacificus* Müll.Arg. *P. samarensis* Müll.Arg. and *P. tenuipes* C.B.Rob., see Chen et al. 2009; Wu et al. 2016). Most species in *Phyllanthus* have a phyllanthoid branching type, which is characterised by flowerless penultimate axes (generally the main, vertical branches) with cataphylls (reduced leaves) and deciduous and floriferous ultimate axes (side branches) bearing real leaves of limited growth (Webster 1956; Radcliffe-Smith 1987), but *Macraea* species have unspecialized non-phyllanthoid branching (Webster 1956; Kathriarachchi et al. 2006). Their axes are not differentiated, flowers occur on any node and leaves instead of cataphylls are present on the penultimate axes (Webster 1956). Non-phyllanthoid branching has evolved several times within *Phyllanthus* (see Kathriarachchi et al. 2006), which resulted in some clades with a morphology similar to the species in subgenus *Macraea*, that are currently placed in other subgenera and sections.

Other subgenera and sections morphologically most similar to *Macraea* are *Phyllanthus* subgenus *Phyllanthus* section *Lysiandra* (F. Muell.) G.L.Webster, *P.* subgenus *Ceramanthus* (Hassk.) Jean F.Brunel, *P.* subgenus *Betsileani* (Jean F.Brunel) Ralim. & Petra Hoffm., *P.* subgenus *Isocladus* G.L.Webster p.p., *P.* subgenus *Phyllanthus* section *Loxopodium* G.L.Webster, *P.* subgenus *Isocladus* G.L.Webster section *Antipodanthus* G.L.Webster and *P.* subgenus *Phyllanthus* section *Salviniopsis* Holm-Nielsen ex Jean F.Brunel. Species of section *Lysiandra* are restricted to Australia and are monoecious or dioecious, with non- or subphyllanthoid branching, and can be distinguished from *Macraea* by their spirally arranged leaves, thicker, opaque, narrow stipules without cordate or auriculate base, thickened anther connectives in some species, the minutely striate or smooth seed surface (Webster 1978; Barret & Telford 2015) and tricolporate pollen (Webster 1978). *Phyllanthus* subgenus *Ceramanthus* is both morphologically and phylogenetically very close to *Macraea* (Kathriarachchi et al. 2006). This subgenus occurs in Africa and Asia and can be distinguished from *Macraea* by the connate filaments and anther connectives with usually elongated anthers, thick and/or urceolate disc of the pistillate flowers that often folds over the ovary (Brunel 1987) and the pollen, which are pantoporate or pantocolporate (Punt 1972). In vegetative state, it is very similar to *Macraea*, but with the leaves on the distal parts of the main axes spirally arranged (Brunel 1987). *Phyllanthus* subgenus *Betsileani,* formerly section *Praemacraea* of subgenus *Macraea* (Brunel 1987), has perisyncolporate pollen (Ralimanana & Hoffmann 2011). It is vegetatively very similar to *Macraea,* but the leaves are spirally arranged at the basal nodes and are only distichous distally. Species of subgenus

Betsileani are found in Madagascar (Ralimanana & Hoffmann 2011). *Phyllanthus* subgenus *Isocladus* is currently monotypical (despite placement of similar species in the group by Brunel 1987), only containing *Phyllanthus maderaspatensis* L., of which the leaves are arranged spirally over its entire length. The filaments of the staminate flower are entirely fused (Brunel 1987, Ralimanana & Hoffmann 2011) and the pollen is colporate (Wu et al. 2016). *Phyllanthus* subgenus *Phyllanthus* section *Loxopodium* occurs in South America, while *Macraea* occurs in Africa, Asia, Polynesia, Australia and the Pacific Islands. Section *Loxopodium* is distinguished by its oblong tetracolporate pollen grains (Webster 1955, 1956). *Phyllanthus* subgenus *Isocladus* section *Antipodanthus* is distinguishable from *Macraea* by its spirally arranged leaves and tri- or tetracolporate pollen (Webster 2002); it occurs in South America and Australia (Webster 2002). *Phyllanthus* subgenus *Phyllanthus* section *Salviniopsis* is a monotypic section containing the only free-floating aquatic species in the *Phyllanthaceae*, the South American *P. fluitans* Benth. ex Müll.Arg., which is very easily recognizable (Brunel 1987). This species has leaves with inflated blades and roots can be found on all axes.

Over the years, reviews, descriptions and keys have been made of *Macraea* for specific regions, for example for New Guinea (Webster & Airy Shaw 1971), Tropical Africa (Brunel 1987), Eastern Melanesia (Webster 1986), French Polynesia (Florence 1997) and Australia (Hunter & Bruhl 1997; Barrett & Telford 2015). The most widespread and complex species of *Macraea, P.virgatus*, is included several times in these reviews. *Phyllanthus virgatus* is morphologically very variable, both within and between regions (Webster & Airy Shaw 1971; Hunter & Bruhl 1997), which has lead to the creation of several varieties and subspecies over time. Many specific and intraspecific taxa have been synonymized with *P. virgatus*, some possibly unjustly (Hunter & Bruhl 1997). A list of these synonyms can be found in Govaerts et al. (2000). Despite the reviews focusing on specific regions, no complete revision of the subgenus has been made until now. A complete revision is very useful in determining and comparing difficult to distinguish and/or related species, as well as comparing *Macraea* to related clades. Here we attempt to completely revise subgenus *Macraea* over its entire distribution. The species included here were either already placed in subgenus *Macraea* by previous authors (e.g. Wight 1852; Webster 1986; Brunel 1987; Hunter & Bruhl 1997) or found to be a part of this group in phylogenetic (Kathriarachchi et al. 2006; Luo et al. 2011a) or palynological studies (e.g. Chen et al. 2009; Wu et al. 2016). Some morphologically similar species like *P. hakgalensis* Thwaites ex Trimen, *P. pseudoparvifolius* R.L.Mitra & Sanjappa and *P. sanjappae* Chakrab. & M.Gangop. might also belong in subgenus *Macraea*, but this has not yet been confirmed by other research, and material of these species was not available during this study. Previous authors placed them in Webster's broad definitions of subgenus *Isocladus* and subgenus *Phyllanthus* (e.g., Balakrishnan & Chakrabarty 2007), but these were shown to be polyphyletic in Kathriarachchi et al. (2006) and their placements should be re-evaluated.

Morphologically important characters

Species can be distinguished by the following morphological characters: habit, indumentum, leaf size and shape, shape of the leaf base, margin and apex, venation, pedicel length and several characters of the flower, such as perianth number, form of the disc (nectar) glands, number of stamens and whether the filaments are free or connate. Ornamentation of fruits and seeds can be variable within species, but sometimes serves as a diagnostic character.

Habit

All species are woody, however some of the smaller species appear to be herbs in the early stages of life. Species found in the Philippines and the Pacific can grow to be small trees of up to 15 meters.

Indumentum

Most species of subgenus *Macraea* are glabrous with some exceptions. Often the indumentum is only present on young branches, but some species always show indumentum (e.g., *P. macraei* Müll.Arg., *P. tararae* Verwijs and *P. wheeleri* G.L.Webster). The indumentum consists of short simple hairs, often appearing as puberulous.

Leaf morphology

Leaves are always arranged alternate and distichous. Contrary to most other species of *Phyllanthus*, leaves can be found on all axes. Each leaf has two stipules at the base. The stipules are triangular, ovate or (sub)orbicular, usually glabrous, persistent or caducous. The stipule base is either straight or auriculate and the margins are often brown, entire and brittle.

The leaves are shortly petiolate, sometimes appearing sessile. The petioles are not thickened or pulvinate, and pubescent or glabrous depending on the species.

The leaves have a pinnate venation, whereby the secondary veins loop and anastomose near the margins. The midvein and secondary veins can be somewhat elevated on either side of the leaf. The blade can be papery to coriaceous with an entire, sometimes revolute margin. The leaf blades are orbicular, lanceolate, ovate to elliptic-oblong. The base of the blades varies from cordate to attenuate, while the apex similarly varies from retuse/emarginate to acuminate.

Inflorescences and flowers

Staminate and pistillate flowers can be found in unisexual or bisexual axillary fascicles, sometimes solitary and then spatially separated. Most species appear to be monoecious (dioecy is found in *P. pacificus* and *P. lancifolius*), however there may be a slight difference in whether staminate or pistillate flowers bloom first.

The perianth consists of 6 sepals in both sexes (except 4 in the staminate flowers of

P. ussuriensis Rupr. & Maxim. and 5 in *P. aoraiensis* Nadeaud). Sepals are usually elliptic to somewhat (ob)ovate and are arranged in two whorls that may differ slightly. Officially the term tepal should be used here instead of sepal, but we like to be consistent with all literature and, therefore, use the term sepal.

The staminate disc consists of free glands with the same number as the sepals and they alternate with the sepals. Staminate flowers have no pistillode and usually have three free stamens (connate in *P. womersley*i Airy Shaw & G.L.Webster and variably connate in *P. prominulatus* J.T.Hunter & J.J.Bruhl and *P. ridsdalei* R.W.Bouman & Verwijs). Each stamen has two thecae, which are rounded to oval and dehisce longitudinally and latrorse with the filaments deflexed so that the anthers are horizontally.

Pistillate flowers have no staminodes and often longer pedicels than the staminate flowers. The pistillate disc is usually entire, but consists of free glands in several species and may show some ornamentation. The ovary is 3-locular with 2 ovules per locule, usually subglobose and shows 6 grooves via which the capsule later opens. On top of the ovary a style can be present, but the three stigmas can also be sessile. Each stigma is bifid at the tip, but the length varies between species.

Fruits and seeds

Pistillate pedicels often become longer in fruit and are slender. The fruits are dry capsules that open septicidally and loculicidally along 6 lines which are usually already visible in flower. The fruits are usually smooth, sometimes verrucose or slightly tuberculate and can be glabrous to hirtellous. All species have typical *Phyllanthaceae* fruits with two seeds per locule. The seeds are trigonous in outline with convex outer walls that are either smooth or verrucate, with the verrucae arranged along longitudinal lines or in random directions.

Biogeography

Subgenus *Macraea* is mainly distributed in the palaeotropics and the species can be found in Africa, Asia and on several island groups in the pacific to Hawai’i. Africa has only one species of subgenus *Macraea*, while in Asia there are roughly 14 species. The subgenus appears to be absent from Madagascar, but a group with a similar flower morphology and habit has evolved there independently (subgenus *Betsileani*, which was so similar that it was formerly included in subgenus *Macraea* (Brunel 1987)). Two examples of morphologically variable island species can be found in *P. pacificus* and *P. distichus*, which either vary in leaf shape or size.

In the phylogeny of Kathriarachchi et al. (2006), several species of subgenus *Macraea* were included, but mainly from Sri Lanka, New Caledonia and Australia. Species from Sri Lanka appeared to be sister to the rest of subgenus *Macraea*, but no species from Africa or the pacific were included.

Taxonomic treatment

This study was performed at the National Herbarium Netherlands (L), with specimens loaned from the Queensland Herbarium (BRI), Australian National Herbarium (CANB), University of California Davis Center for Plant Diversity (DAV), Conservatoire et Jardin botaniques de la Ville de Genève (G), Harvard University Herbaria (A), Royal Botanic Gardens Kew (K), Naturalis Biodiversity Center (L), Missouri Botanical Garden (MO), Royal Botanic Gardens, National Herbarium of New South Wales (NSW), Muséum National d'Histoire Naturelle (P), Swedish Museum of Natural History (S) and United States National Herbarium, Smithsonian Institution (US). All type specimens cited here were either seen as physical specimens or as high quality scans online. When type specimens were mentioned in literature, but could not be traced, they are denoted with a question mark or "not seen" in the citation. Barcodes are mentioned when a particular herbarium houses several duplicates of a type specimen to provide a unique identifier.

Phyllanthus subgenus **Macraea** (Wight) Jean F.Brunel

Phyllanthus subgenus *Macraea* (Wight) Jean F.Brunel (1987) 293. —*Macraea* Wight (1852) 27. — *Phyllanthus* section *Macraea* (Wight) Baill. (1858) 628; Müll.Arg. (1866) 384; G.L.Webster (1986) 93. — Lectotype (designated by Webster 1986): *Macraea oblongifolia* Wight (= *P. virgatus* G.Forst).

Erect or prostrate herbs, subshrubs, shrubs or trees, monoecious or dioecious; branching non-phyllanthoid; branches (minutely) ridged or smooth, brown, distally often flattened and/or winged, often green; (aerial roots occasionally present on nodes in *P. womersleyi*). *Indumentum* absent or short, simple hairs present on (distal parts of the) branches, leaves, petioles, pedicels and ovaries. *Stipules* triangular, ovate or (sub)orbicular, flat, membranous, translucent chestnut-brown, persistent, base often auriculate. *Leaves* alternate, distichous, simple, petiolate; blade elliptic, (ob)ovate or (sub)orbicular, margin entire, glabrous, (hairy on both sides in *P. tararae* and *P. wheeleri*); midrib sunken to prominent above, flat or prominent underneath, lateral veins often barely visible, looping and anastomosing near the margin, flat or prominent on both sides. *Inflorescences* axillary fascicles, unisexual, (rarely) bisexual in some species. *Staminate flowers* solitary to 12 together, bracteate; pedicel glabrous; sepals 6 (except 5 in *P. aoraiensis* and sometimes 4 in *P. ussuriensis*), elliptic or (ob)ovate, sometimes in two whorls with sepals differing in size and/or shape, imbricate; disc glands alternating with and as many as sepals, circular, flat; stamens 3 (sometimes 2 in *P. ussuriensis*), filaments free (connate in *P. womersleyi* and variably connate in *P. prominulatus* and *P. ridsdalei*), often reflexed, thecae 2, (sub)globular or (sub)ovoid, dehiscencing latrorse via longitudinal slits (pollen: Punt 1980; Wu et al. 2016). *Pistillate flowers* solitary to

7 together, bracteate; sepals 6, elliptic or (ob)ovate, sometimes in two whorls with sepals differing in size and/or shape, imbricate; disc annular (6 disc glands in *P. dumosus*, *P. tenuipes*, *P. ussuriensis*, *P. wheeleri* and *P. womersleyi*, then alternating with sepals), flat; ovary 3-locular (rarely 4-locular in *P. lancifolius*), glabrous or pubescent; ovules 2 per locule; style absent to present, stigmas 3, spreading, bifid for between half to 4/5 of the length, reflexed. *Fruits* capsules, subglobular or oblate, 6-grooved, in some species with 3 grooves deeper than the others and/or bivalved, glabrous or (minutely) verrucate; stigmas and sepals persistent; columella narrowly tetrahedriform, persistent after dehiscense. *Seeds* trigonous, triangular in transverse section, with convex outer wall, smooth or verrucate, verrucae circular (or rhomboid and stretched widthwise in *P. myrtifolius*), sometimes very small, randomly placed or in indistinct longitudinal lines.

Key to the species

1. Stems barely branched, arising from a thick woody rhizome. Staminate disc glands often bell-shaped — Africa..9. *P. glaucophyllus*
1. Stems usually branched several times, growing without a thick rhizome. Staminate disc glands flattened — outside Africa 2

2. Ovary on a gynophore. Stigmas united into a style for 0.3–0.6 or 1.5–1.6 mm, then spreading into 3 separate lobes, latter complete bifid or with bifid tips..3
2. Ovary sessile, without gynophore. Stigmas only basally united or entirely free 4

3. Branches glabrous; internodes 6–7 mm long. Staminate sepals 1.5–2 by 0.8–1 mm; filaments variably connate. Pistillate disc annular. Style 1.5–1.6 mm high, stigmas 1–2 mm long with bifid tips...................................16. *P. ridsdalei*
3. Branches pubescent; internodes 2–4 mm long. Staminate sepals 1–1.1 by c. 0.5 mm; filaments free. Pistillate disc consisting of 6 free glands. Style 0.3–0.6 mm high, stigmas 0.2–0.5 mm long, completely bifid.................19. *P. tenuipes*

4. Leaf margin thickened, flat 5
4. Leaf margin not thickened, flat or revolute 7

5. Stipules 0.5–0.7 mm long. Stamens up to 0.4 mm long; filaments sometimes connate. Pistillate pedicel 0.3–1.1 mm long; sepals 0.3–0.7 by 0.2–0.5 mm; stigmas 0.2–0.3 mm long. Fruits 1.5–1.8 mm in diam ....15. *P. prominulatus*
5. Stipules 1–2 mm long. Stamens longer than 0.5 mm; filaments free. Pistillate pedicel 1.5–10 mm long; sepals 1–1.5 by 0.5–0.1 mm; stigmas c. 1 mm long. Fruits more than 2.2 mm in diam...6

6 Petioles 0.2–1 mm long; leaf base rounded or obtuse, apex not mucronate, lateral veins 3–5 on each side of the midrib. Staminate pedicels 1–1.5 mm long. Pistillate pedicels 1.5–2.5 mm long. Seeds 1.2–2 mm long .... 2. *P. chrysanthus*
6 Petioles 1–1.5 mm long; leaf base oblique, subcordate, apex mucronate, lateral veins 5–7 on each side of the midrib. Staminate pedicels 2–4 mm long. Pistillate pedicels 8–10 mm long. Seeds c. 2.5 mm long ....9. *P. glaucophyllus*

7. Branches and/or leaves least partially hairy (check young parts)....................8
7. Branches and leaves completely glabrous 15

8. Pistillate disc consisting of free glands, alternating with sepals........................9
8. Pistillate disc entire, annular.. 10

9. Internodes 0.8–1 mm long. Leaf blades 2–7 by 1.5–3.5 mm. Stamens c. 0.4 mm long. Ovary glabrous. Fruiting pedicels 8–12 mm long........5. *P. dumosus*
9. Internodes 2–5 mm long. Leaf blades 5–13.5 by 2–7 mm. Stamens c. 0.6 mm long. Ovary densely hirsute. Fruiting pedicels 3–4 mm long..... 23. *P. wheeleri*

10. Leaf blades densely hairy on both sides, less than 4 mm wide, lateral veins not visible .... 18. *P. tararae*
10. Leaf blades glabrous, sometimes distally tomentellous above (*P. samarensis*) or (sparsely) hairy (*P. lancifolius*)/ rarely tomentellous (*P. samarensis*) on both sides, wider than 4 mm, lateral veins 6–11, well visible on each side of the midrib 11

11. Staminate flowers c. 4 mm diam. Pistillate flower 4–5 mm in diam. Ovary verrucate ....11. *P. macraei*
11. Staminate flowers 1–3 mm diam. Pistillate flower up to 3 mm in diam. Ovary hairy, tuberculate or glabrous... 12

12. Stipule margins fimbriate. Leaf blades obovate, sometimes elliptic, base narrowly cuneate to attenuate .... 3. *P. clarkei*
12. Stipule margins entire. Leaf blades elliptic to oblong or ovate-elliptic, base obtuse, sometimes cuneate, rounded to subcordate....................................... 13

13. Leaf blades mostly ovate-elliptic, 9–79 mm long, apex acuminate... 10. *P. lancifolius*
13. Leaf blades mostly elliptic to oblong, 7–38 mm long, apex acute to obtuse or rounded to retuse 14

14. Leaf blades 11–38 mm long; stamens 0.6–0.8 mm long. Fruiting pedicels

11–25 mm long...6. *P. everettii*

14. Leaf blades 7–24 mm long; stamens c. 0.3 mm long. Fruiting pedicels not longer than 11 mm...17. *P. samarensis*

15. Branches strongly winged, wings 0.8–1 mm wide. Flowers of both sexes with 5 sepals...1. *P. aoraiensis*

15. Branches not winged, ridged or slightly (up to 0.2 mm wide) winged. Flowers of both sexes usually with 6 sepals (but often 4 in the staminate flowers of *P. ussuriensis*)... 16

16. Usually prostrate herbs or subshrubs, sometimes erect up to 150 cm high. Stamen filaments connate, but connectives free. Leaf blade irregularly orbicular, 2–4 mm in diam.. 24. *P. womersleyi*

16. Usually erect herbs, (sub)shrubs or trees. Stamen filaments free. Leaf blade suborbicular, ovate, oblong, elliptic, obovate, 2–85 mm long 17

17. Leaf blades obovate, base very narrow, cordate-sagittate........13. *P. myrtifolius*

17. Leaf blades suborbicular, ovate, elliptic, oblong or seldom obovate, base of normal width, cuneate, attenuate, rounded, obtuse or (sub)cordate 18

18. Pistillate disc consisting of free glands.. 19

18. Pistillate disc entire, annular.. 20

19. Leaf blades 2–7 by 1.5–3.5 mm, blades only 1.3–2 times longer than wide; apex retuse to rounded. Staminate flowers with 6 sepals, stamens 3 ....5. *P. dumosus*

19. Leaf blades 4–25 by 1.5–8 mm, blades >2 times longer than wide; apex obtuse or acute, rarely rounded. Staminate flowers with 4 or 6 sepals, stamens mostly 2, but sometimes 3 on the same plant ....21. *P. ussuriensis*

20. Leaf blades 22–85 by 10–40 mm, midrib prominent on both sides, lateral veins prominent above. Pistillate pedicels up to 30 mm long . 20. *P. urceolatus*

20. Leaf blades 2–80 by 1–32 mm, midrib above flat or sunken (sometimes slightly prominent), prominent underneath, lateral veins flat above or sunken or barely visible. Pistillate pedicels up to 19 mm long 21

21. Staminate flowers 1.5–4 mm in diam. Pistillate flowers 4–5.5 mm in diam.. 22

21. Staminate flowers 0.7–1.7 mm in diam. Pistillate flowers 1–3 mm in diam.. 24

22. Leaf blades 3–37 by 2.5–18 mm. Staminate flowers 1.5–2.8 mm in diam..........

....8. *P. gardnerianus*

22. Leaf blades 7–80 by 4–32 mm. Staminate flowers 3–4 mm in diam 23

23. Large shrubs or trees, 0.9–5 m high. Petioles up to 4 mm, leaf blades 7–80 by 5–32 mm. Staminate pedicels 1.5–3 mm long ....4. *P. distichus*
23. Shrubs to herbs, usually less than 1 m high (exceptionally 2 m in *P. pacificus*). Petioles usually shorter than 2 mm, leaf blades 14–45 by 4–18 mm. Staminate pedicels 3–6 mm long ....11. *P. macraei*

24. Staminate pedicels 0.5–0.8 mm long. Pistillate flowers 1–1.2 mm in diam, pedicels 0.5–2 mm long .... 12. *P. minutiflorus*
24. Staminate pedicels 0.2–5 mm long. Pistillate flowers more than 1.5 mm in diam, pedicels at least 2.5 mm long 25

25. Leaf blades wider than 6 mm, 1.1–3.7 times longer than wide. Staminate sepals 1.2–1.5 by 1–1.2 mm; stamens 1–1.2 mm long..................14. *P. pacificus*
25. Leaf blades at most 6 mm wide; (1–)2.5–7.5 times longer than wide. Staminate sepals 0.4–1 by 0.2–0.5 mm; stamens 0.3–0.4 mm long.................................. 26

26. Leaf blades 6–15 by 1–2 mm. Stipules suborbicular, c. 0.5 by 0.3 mm. Leaf blades small, not longer than 15 mm, usually 5–7.5 times longer than wide, lateral veins barely visible. Staminate flowers c. 0.8 mm in diam. Pistillate pedicels 2.5–4 mm long, ovaries always verrucate ....7. *P. exilis*
26. Leaf blades 3–40 by 1–6 mm. Stipules triangular, 1–2.5 by 0.5–1 mm. Leaf blades small to slightly larger, 3–40 mm long, mostly less than 5 times longer than wide (rarely up to 6.7 times), venation prominent, usually 5–8 lateral veins on each side of the midrib. Staminate flowers 0.8–1.7 mm in diam. Pistillate pedicels 3–9 mm long, ovaries glabrous or verrucate ..22. *P. virgatus*

1. **Phyllanthus aoraiensis** Nadeaud — Map 4-1

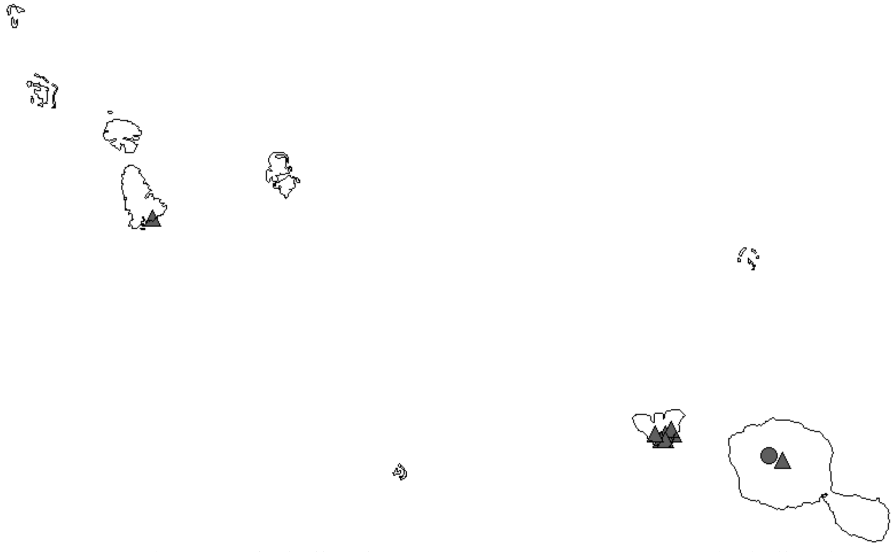
Phyllanthus aoraiensis Nadeaud (1873) 73; Drake (1892) 286; (1893) 181; J.Florence (1997) 122; W.L.Wagner & Lorence (2011) 69. — Lectotype (designated by Florence 1997): *J. Nadeaud 459* (P (P00636870); iso P (P00636871 & P00636872), G), Tahiti.

Shrubs, 2–3 m high, monoecious; branches glabrous, strongly winged, wings 0.8–1 mm wide; internodes 11–26 mm long. *Stipules* triangular, scarious, c. 0.8 mm long, caducous, flat, thin, base auriculate, margin entire, apex acute. *Leaves*: petiole 1–3 mm long, glabrous; blade ovate-oblong, 45–125 by 17–47 mm, 2.2–3.3 times longer than wide, subcoriaceous, glabrous, base (sub)cordate, weakly asymmetric, margin thickened, apex acute; midrib flat on both sides, lateral veins 9–11 on each side, flat. *Staminate flowers* few, axillary, c. 0.7 mm in diam; pedicel 10–20 mm long, glabrous,

thicker than pistillate one; sepals 5, red, in two indistinct whorls, ovate, apex obtuse, recurved; disc glands 5; stamens 3, fusion of filaments unknown, thecae rounded. *Pistillate flowers* solitary, axillary; pedicel >20 mm long, sepals 5, red, in two indistinct whorls, oblong, 1–2 mm high, apex acute; disc entire, weakly lobed; ovary sessile, with each locule grooved; style absent, stigmas 3, bifid, recurved. *Fruits* 4–5 mm in diam, 6-grooved, glabrous; pedicel 12–30 mm long; columella 1.3–1.9 mm long. *Seeds* 4–5 mm long, verrucate, verrucae not known in detail.
Distribution — Endemic to Tahiti (Aorai mountain).
Habitat & Ecology — Found on mountains at 1000 m altitude. Flowering and fruiting in November (based on only the type collection).
Note — A species morphologically very close to *P. urceolatus* and tentatively placed here in subgenus *Macraea*. This species is endemic to Tahiti, but has not been collected since 1857 and is presumed extinct (Florence 1997; Wagner & Lorence 2011). *Phyllanthus aoraiensis* is easily distinguished from *P. urceolatus* and *P. pacificus* by the very large wings on the branches, the larger seeds and its red flowers. Unfortunately, only the type material was available online, thus descriptions of fruits and flowers have been completed from literature (e.g. Florence 1997).

2. Phyllanthus chrysanthus Baill. — Map 4-2

Phyllanthus chrysanthus Baill. (1862a) 238; Müll.Arg. (1863) 34; (1866) 393; Guillaumin (1948) 177; Lobr.-Callen et al. (1988) 294; M.Schmid (1991) 48. — *Diasperus chrysanthus* (Baill.) Kuntze (1891) 598. — Lectotype (designated by Schmid 1991): *E. Vieillard 1201*, 1855 (P (P00066057); iso P (P00066058)), New



Map 4-1. Distribution of *Phyllanthus aoraiensis* Nadeaud (•) and *Phyllanthus urceolatus* Baill. (•) in French Polynesia.

Caledonia, Balade.
Phyllanthus persimilis Müll.Arg. (1863) 34; (1866) 392. — Lectotype (designated here): *E. Vieillard 1201* p.p., 1855 (G-DC (G00318228)), New Caledonia, Balade.

(Prostrate) shrubs, 10–100 cm high, monoecious; branches (minutely) ridged, brown, older branches subcylindrica, glabrous, younger branches subcylindrical or distally flattened, often winged and shortly puberulous; internodes 0.2–4 mm long. *Stipules* triangular, 1–2 by 0.5–1 mm, base bilaterally auriculate, margin entire or (extremely) erose, apex attenuate. *Leaves*: petiole 0.2–1 mm long, glabrous; blade elliptic or orbicular, 1.5–30 by 1–9 mm, 1–2.5(–5) times longer than wide, base rounded or obtuse, margin thickened, flat, apex rounded or obtuse, not mucronate; midrib slightly prominent above, prominent underneath, lateral veins 3–5 on each side, often not or barely visible, flat on both sides. *Staminate flowers* 1–3 together, 1.3–2 mm in diam; pedicel 1–1.5 mm long, glabrous; sepals 6, elliptic, 0.5–1.2 by 0.2–0.8 mm, whitish, (pale) green or (pale) yellow, apex acute or obtuse; disc glands 6, circular, 0.2–0.3 mm in diam, flat; stamens 3, 0.5–0.8 mm long, filaments free, thecae subglobular, c. 0.2 mm long. *Pistillate flowers* solitary, 2–3 mm in diam; pedicel 1.5–2.5 mm long, glabrous; sepals 6, elliptic, 1–1.5 by 0.5–0.8 mm, whitish, (pale) green or (pale) yellow, apex obtuse or rounded; disc annular, (slightly) lobed, 0.8–1 mm in diam, c. 0.1 mm high; ovary sessile, oblate(-ovoid), 0.6–1 mm in diam, 0.4–0.8 mm high, glabrous; style absent, stigmas 3, c. 1 mm long, bifid for between 3/4 and 4/5 of the length, reflexed. *Fruits* subglobular, 2.2–3 mm in diam, with 3 deep and 3 shallow grooves, often bivalved, glabrous, green or red; pedicel 2–3.5 mm long, glabrous; columella 0.8–1 mm long. *Seeds* 1.2–2 mm high, c. 1 mm wide, minutely verrucate, chestnut-brown, verrucae circular, randomly placed or in (indistinct) longitudinal lines.
Distribution — New Caledonia.
Habitat & Ecology — Occuring in maquis shrubland, forests and near rivers, on rocky, alluvium, laterite and/or serpentine soils. Altitude: 0–1150 m. Flowering and fruiting the whole year round.
Note — According to Guillaumin (1948), *P. chrysanthus* can be distinguished by its randomly positioned verrucae on the seeds and the smooth ovary, while *P. virgatus* from New Caledonia has seeds with the verrucae in a linear pattern and the ovary can be either smooth or verrucate. However, seeds with randomly positioned verrucae have been found in specimens of *P. virgatus* from all over Asia and Australia, not just from New Caledonia. A better distinctive character is the thickened leaf margins, in comparison to the flat or revolute leaf margins of *P. virgatus*, and the more prominent midvein in *P. chrysanthus*.

Key to the varieties

1.Branches glabrous, flattened, especially distally. Leaf blades (2–)5–19(–30) mm

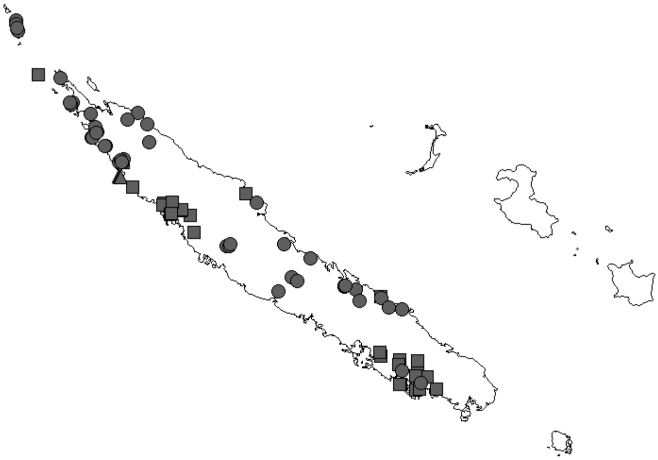
longa. var. *chrysanthus*
1.Young branches distally shortly puberulous or minutely verrucate, subcylindrical, only slightly flattened. Leaf blades 1.5–10 mm long 2

2.Leaf blades 1.5–3.5(–5) by 1–2 mm. Staminate sepals c. 1.2 mm long. Pistillate sepals c. 1.5 mm long ....b. var. *deverdensis*
2.Leaf blades 3.5–10 by 2.5–8 mm. Staminate sepals 0.5–0.8 mm long. Pistillate sepals 1–1.2 mm long .... c. var. m*icrantheoides*

a. var. **chrysanthus**

Phyllanthus chrysanthus Baill. var. *chrysanthus*: M.Schmid (1991) 50.

Shrubs, 10–70 cm high; fertile branches minutely ridged, glabrous, distally flattened and winged; internodes 2–4 mm long. *Stipules* 1.5–2 by 0.8–1 mm, margin entire or (extremely) erose. *Leaves*: petiole c. 1 mm long; blade elliptic, (2–)5–19(–30) by (1–)2–9 mm, 1.6–2.1(–5) times longer than wide, glabrous, upper surface dark



Map 4-2. Distribution of *Phyllanthus chrysanthus* Baill. var. *chrysanthus* (•), *P. chrysanthus* var. *deverdensis* M.Schmid (•) and *P. chrysanthus* var. *micrantheoides* (Baill.) M.Schmid (•) on New Caledonia.

green, underneath pale greyish green, sometimes reddish, especially in young leaves, base rounded or obtuse, apex rounded, rarely obtuse; lateral veins flat above, barely visible underneath. *Staminate flowers* solitary to 3 together, 1.3–2 mm in diam; pedicel 1–2 mm long; sepals 0.8–1 by 0.3–0.6 mm, (pale) green or yellow, apex acute or obtuse; disc glands 0.2–0.3 mm in diam; stamens 0.5–0.7 mm long. *Pistillate flowers* c. 2 mm in diam; pedicel 1.5–2.5 mm long; sepals 1–1.2 by 0.5–0.6 mm, (pale) green or yellow, apex ovate; disc annular, with six small lobes alternate to the sepals, c. 0.8 mm in diam, c. 0.1 mm high; ovary oblate-ovoid, c. 0.6 mm in diam, c. 0.4 mm high; stigmas c. 1 mm long, bifid for 3/4 of the length. *Fruits* 2.2–3 mm in diam, green, yellow or red; pedicel 2–3.5 mm long; columella c. 0.8 mm long. *Seeds* c. 1.5 mm high, c. 1 mm wide, verrucae circular, in longitudinal lines.
Distribution — New Caledonia.
Habitat & Ecology — Occuring in (high) maquis shrubland and forests, on rocky, alluvium and/or serpentine soils. Altitude: 0–1150 m.

b. var. **deverdensis** M.Schmid

Phyllanthus chrysanthus Baill. var. *deverdensis* M.Schmid (1991) 53. — Type: *H.S. MacKee 30021* (holo P (P00066096); iso K, NOU, P (P00066097)), New Caledonia, Cap Deverd, Gomen.

Prostrate shrubs; branches subcylindrical, older branches ridged, glabrous, younger branches without ridges, shortly puberulous; internodes 0.2–1 mm long. *Stipules* c. 1.5 by 0.8 mm, margin entire. *Leaves*: petiole c. 0.2 mm long; blade elliptic or orbicular, 1.5–3.5(–5) by 1–2 mm, 1–2 times longer than wide, glabrous, green, base rounded, apex rounded or obtuse; lateral veins not visible. *Staminate flowers* solitary or 2 together, c. 2 mm in diam; pedicel c. 1 mm long; sepals c. 1.2 by 0.8 mm, whitish or pale green, apex obtuse; disc glands c. 0.2 mm in diam; stamens c. 0.8 mm long. *Pistillate flowers* c. 3 mm in diam; pedicel 2–2.5 mm long; sepals c. 1.5 by 0.6 mm, whitish or pale green, apex obtuse; disc and ovary not seen. *Fruits* not seen intact; pedicel 2–2.5 mm long; columella c. 1 mm long. *Seeds* c. 1.2 mm high, c. 1 mm wide, verrucae circular, randomly placed or in indistinct longitudinal lines.
Distribution — New Caledonia (Kaala-Gomen, Cap Deverd).
Habitat & Ecology — Maquis shrubland and forests. Altitude: 20—30 m.
Note — No complete pistillate flowers or intact fruits were found in the six specimens studied.

c. var. **micrantheoides** (Baill.) M.Schmid

Phyllanthus chrysanthus Baill. var. *micrantheoides* (Baill.) M.Schmid (1991) 52. — *Phyllanthus micrantheoides* Baill. (1862a) 238; Müll.Arg. (1866) 387. — *Diasperus micrantheoides* (Baill.) Kuntze (‘*micrantheodes*’) (1891) 600. — Lecotype (designated

here): *J.F. Pancher 365* (P (P00066093); iso P (P00066094)), New Caledonia, Sommet du Pic.
Phyllathus rufidulus Müll.Arg. (1863) 29; Guillaumin (1948) 176. — *Diasperus rufidulus* (Müll.Arg.) Kuntze (1891) 600. — Syntypes: *E. Vieillard 1196* (G-DC, P), New Caledonia, Port de France.
Phyllanthus rufidulus Müll.Arg. var. *kafeateenis* Guillaumin (1962) 247. — Lectotype (designated by Schmid 1991): *A. Guillaumin & M. Baumann 9657* (probably P, not seen), New Caledonia, Mont Kafeate.

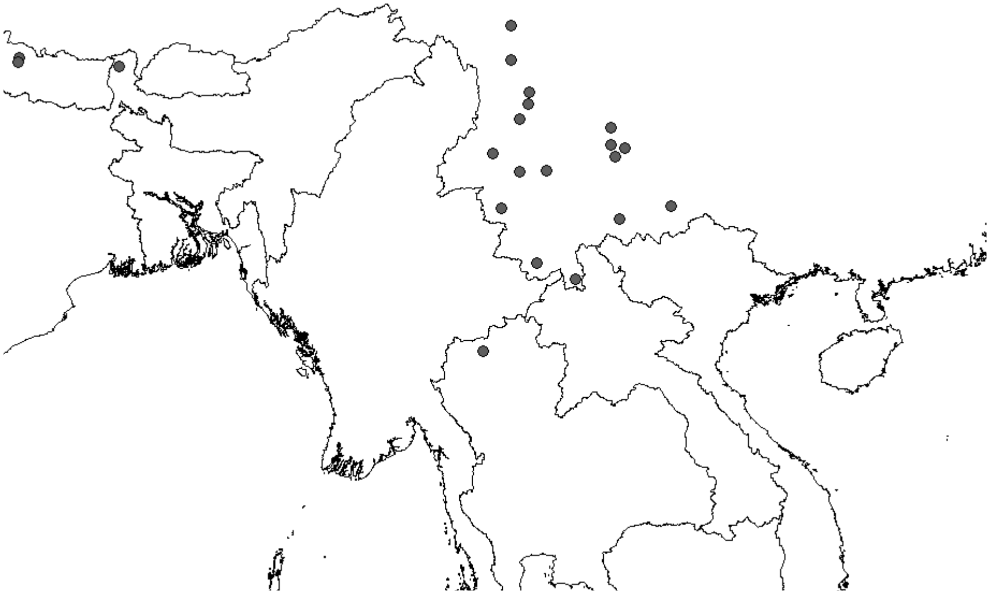
Shrubs, 10–100 cm high; branches subcylindrical, older branches glabrous, ridged, younger branches without ridges, sometimes distally slightly flattened, shortly puberulous or minutely verrucate; internodes 0.2–1 mm long. *Stipules* c. 1 by 0.5 mm, margin entire. *Leaves*: petiole c. 0.3 mm long; blade elliptic, ovate or orbicular, 3.5–10 by 2.5–8 mm, 1.2–2.5 times longer than wide, glabrous, rarely puberulous on one or both sides, upper surface light to dark green, underneath paler green, sometimes reddish on one or both sides, base rounded, apex rounded or obtuse; lateral veins 3–5 flat and barely visible on both sides. *Staminate flowers* solitary to 3 together, 1.2–2 mm in diam; pedicel 1–1.4 mm long; sepals 0.5–0.8 by 0.2–0.5 mm, (pale) green or yellow, often with reddish centre, apex acute; disc glands c. 0.2 mm in diam; stamens c. 0.5 mm long. *Pistillate flowers* c. 2.5 mm in diam; pedicel 1.5–2.5 mm long; sepals 1–1.2 by 0.6–0.8 mm, (pale) green or yellow, often with reddish centre, apex obtuse; disc annular, slightly lobed, c. 1 mm in diam, c. 0.1 mm high; ovary oblate, c. 1 mm in diam, c. 0.8 mm high; stigmas 3, c. 1 mm long, bifid for 4/5 of the length. *Fruits* c. 2.2 mm in diam, green or red; pedicel 2–2.5 mm long; columella c. 1 mm long. *Seeds* c. 2 by 1 mm, verrucae circular, randomly placed or in indistinct longitudinal lines.
Distribution — New Caledonia.
Habitat & Ecology — Occuring in (open) maquis shrubland and low forests, often near rivers, on alluvium, laterite and/or serpentine soils. Altitude: 10–1000 m.

3. Phyllanthus clarkei Hook.f. — Map 4-3
Phyllanthus clarkei Hook.f. (1887) 297; A.M.Cowan & Cowan (1929) 117; Croizat (1940) 650; Airy Shaw (1972) 317; R.L.Mitra & Sanjappa (2003) 13; Chantar. in Welzen & Chayam. (2007) 483; P.T.Li & M.G.Gilbert in Z.Y.Wu, P.H.Raven & D.Y.Hong (2008) 181; Chakrab. & N.P.Balakr. (2009a) 527; Chakrab. & N.P.Balakr. (2018) 338. — *Diasperus clarkei* (Hook.f.) Kuntze (1891) 601. — Lectotype (designated by Mitra & Sanjappa 2003): *C.B. Clarke* 25420 (K (K000246582); iso BM (BM000951413), K (K000246581, K000246583)), India, Sikkim Himalaya at Catsuperri.
Phyllanthus simplex Retz. var. *tonkinensis* Beille (1927) 578. — Syntypes: *Balansa s.n.* (probably in P, not traced) Tonkin Cho-bo (black river), Vietnam; *Poilane s.n.* (probably in P, not traced) Ban-sa-noi, Ba-na-punk, Vietnam.

(Sub)shrubs, up to 120 cm high, monoecious; branches terete, not winged, scabrid to puberulous; internodes 2–7 mm long. *Stipules* ovate-triangular, 1.5–2.4 by c. 0.8 mm, persistent, brown when dry, base bilaterally auriculate, margin fimbriate, apex caudate. *Leaves*: petiole 1–1.5 mm long, glabrous; blade obovate, sometimes elliptic, 7–22 by 4–12 mm, 1.2–2.4 times longer than wide, membranous, base cuneate-attenuate, margin entire, plane to revolute, apex rounded to revolute, mucronate, dark green above, light green underneath; midrib flat above, prominent underneath, lateral veins 4 or 5 per side, barely visible above, clear underneath. *Staminate flowers* 1–3 together, 1.5–2.5 mm in diam; pedicel 1–3 mm long, glabrous; sepals 6, obovate, 0.8–1.2 by 0.5–0.9 mm, apex acuminate; disc glands 6, flat, circular, c. 0.2 mm in diam, thin, smooth; stamens 3, 0.7–1 mm long, filaments free, 0.5–0.8 mm long, thecae globular, 0.2–0.3 mm long. *Pistillate flowers* solitary, rarely in pairs, 1.5–2.5 mm in diam; pedicel 2–4 mm long, glabrous; sepals 6, obovate, 1–1.2 by 0.5–0.6 mm, apex obtuse; disc annular, slightly cupuliform, 6-lobed, c. 1.2 mm in diam, 0.2–0.3 mm high, smooth; ovary subglobose, c. 1 mm in diam, c. 0.9 mm high, each locule with a groove, glabrous; stigmas 3, c. 0.8 mm long, bifid for half of length. *Fruits* globose, 2.2–3.2 mm diam by c. 2.5 mm high, 6-grooved, green, turning black when dry, glabrous; pedicel 3–9 mm long; columella c. 1.2 mm long. *Seeds* trigonous, c. 2.2 by 1.1 mm, smooth when young, then verrucate along longitudinal lines, verrucae circular.

Distribution —India, Sri Lanka, Nepal, Myanmar, China, Thailand and Vietnam.

Habitat & Ecology — Open, rocky ground, found in pastures, sometimes on



Map 4-3. Distribution of *Phyllanthus clarkei* Hook.f. in S.E. Asia main land.

limestone ridges. Altitude: 900–2300 m . Flowering and fruiting whole year round.

Vernacular name — Thailand: Mayom doi (มะยมดอย) (Chantaranothai 2007).

Notes — 1. This species is closely related to other species of subgenus *Macraea* according to the phylogeny of Luo et al. (2011a). Morphological characters such as its non-phyllanthoid branching and staminate flowers with free stamens confirm that this species should be placed in subgenus *Macraea*.

2. A similar species was described by Chakrabarty & Gangopadhyay (1993) as *P. sanjappae*. This species has not yet been included in any pollen or phylogenetic study and the staminate flowers are not known, so it is difficult to place this species in subgenus *Macraea* with full certainty. *Phylanthus sanjappae* is distinct by its glabrous branchlets, sessile leaves with a mucron and the presence of a short style under the stigmas. However, the leaves of *P. clarkei* can also be mucronate and the indumentum is variable.

3. This species was confused by Hooker (1887) with *P. parvifolius* Butch.-Ham. ex D.Don and is also similar to *P. pseudoparvifolius*. A detailed study into the identity of these species was done by Mitra & Sanjappa (2003). *Phyllanthus clarkei* can be distinguished from *P. parvifolius* and *P. pseudoparvifolius* by its branching floriferous shoots, completely free stamens and longer fruiting pedicels (Mitra & Sanjappa 2003).

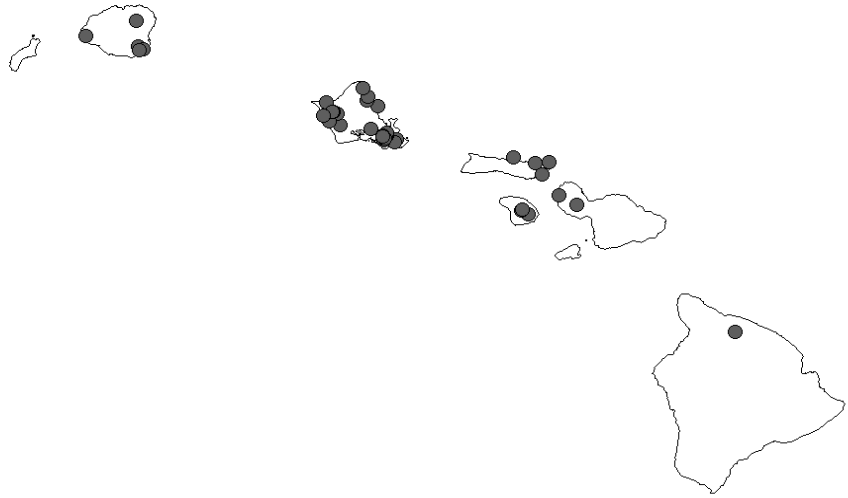
4. Map data was supplemented with data from Gbif.org. Coordinate data can be accessed via DOI.org/10.15468/dl.uv7ddr.

4. Phyllanthus distichus Hook. & Arn. — Map 4-4

Phyllanthus distichus Hook. & Arn. (1832) 95; Müll.Arg. (1866) 413; Hook.f. (1887) 304; W.J.Kress et al. (2003) 233. —*Diasperus distichus* (Hook. & Arn.) Kuntze (1891) 599. — Lectotype (designated here): Beechey's Voyage (*Lay & Collie) s.n.* (K (K001056963), iso E, K (K001056962), L (L.2252054), USA, Hawai'i, O'ahu.
[*Phyllanthus argentatus* Noronha (1790) 22, nom. nud.]
[*Phyllanthus cheremela* Roxb. (1814) 104, nom. nud.]
Phyllanthus sandwicensis Müll.Arg. (1863) 31; (1866) 389; Wawra (1875) 149; Sherff (1939) 563.—*Diasperus sandwicensis* (Müll.Arg.) Kuntze (1891) 600. — *Phyllanthus sandwicensis* Müll.Arg. var. *oblongifolius* Müll.Arg. (1863) 31, nom. inval., not autonym; (1866) 389. — Syntypes: *C. Gaudichaud-Beaupré s.n.* (P), USA, Hawai'i; *L.K.A. Chamisso s.n.* (LE), USA, Hawai'i.
Phyllanthus sandwicensis Müll.Arg. var. *ellipticus* Müll.Arg. (1863) 31; (1866) 389. —*Phyllanthus distichus* Hook. & Arn. var. *ellipticus* (Müll.Arg.) Govaerts & Radcl.-Sm. (1996) 176. — Syntypes (based on Müller 1866): *C. Gaudichaud-Beaupré 290* (G, G-DC, P), USA, Hawai'i; *Chamisso s.n.* (LE)*; B. Seemann 2284* (BM).
Phyllanthus sandwicensis Müll.Arg. var. *parvifolius* Müll.Arg. (1863) 32; (1866) 389. — *Phyllanthus sandwicensis* Müll.Arg. f. *parvifolius* (Müll.Arg.) Wawra (1875) 149.

— Type: *C. Gaudichaud-Beaupré 289* (holo G-DC), USA, Hawai'i.
Phyllanthus sandwicensis Müll.Arg. var. *radicans* Müll.Arg. (1863) 32; (1866) 389. — Type: *C. Gaudichaud-Beaupré s.n.* (holo G-DC), USA, Hawai'i.
Phyllanthus sandwicensis Müll.Arg. f. *grandifolia* Wawra (1875) 149. — Type: *W. Hillebrand 2340a* (holo W), Hawai'i.
Phyllanthus sandwicensis Müll.Arg. f. *rufidus* Fosberg (1936) 6. — Type: *F.R. Fosberg 12410* (holo BISH (BISH1009121); iso BISH (BISH1009120), CAS), USA, Hawai'i, Lanai, Haalelepaakai.
Phyllanthus sandwicensis Müll.Arg. var. *degeneri* Sherff (1939) 567. — *Phyllanthus distichus* Hook. & Arn. var. *degeneri* (Sherff) Govaerts & Radcl.-Sm. (1996) 176. — Type: *O. Degener 8019* (iso F), USA, Hawai'i.

Shrubs or trees, 90–500 cm high, monoecious; branches ridged, glabrous, dark or cinnamon-brown, distally flattened, winged, dark brown or sage-green; internodes 3–10 mm long. *Stipules* ovate, c. 2 by 1 mm, base cordate, margin erose, spinose or very irregular, apex acute. *Leaves*: petiole 0.5–4 mm long, glabrous; blade elliptic, 7–80 by 5–32 mm, 1.3–3.1 times longer than wide, glabrous, upper surface sage-green, sometimes reddish, underneath slightly paler, base rounded, margin not thickened, flat, apex acute, less often obtuse or rounded; midrib flat or sunken above, prominent underneath, lateral veins 5–11 on each side, flat or sunken on



Map 4-4. Distribution *Phyllanthus distichus* Hook. & Arn. in Hawai'i.

both sides, sage-green above, chestnut-brown underneath. *Staminate flowers* solitary to 7 together, c. 3 mm in diam; pedicel 1.5–3 mm long, glabrous; sepals 6, elliptic, c. 1.2 by 0.6 mm, light red with pale yellow margin or entirely pale yellow, apex acute; disc glands 6, circular, c. 0.5 mm in diam, flat; stamens 3, c. 1 mm long, filaments free, reflexed, thecae subglobular, c. 0.3 mm long. *Pistillate flowers* in pairs or solitary, c. 5 mm in diam; pedicel 8–10 mm long, glabrous; sepals 6, elliptic, 2–2.5 by c. 1 mm, light red with pale yellow margin or entirely pale yellow, apex acute; disc annular, with six small lobes alternate to the sepals, crispate, c. 1 mm in diam, c. 0.1 mm thick; ovary sessile, globular-oblate, c. 1.5 mm in diam, c. 1 mm high, glabrous; style absent, stigmas 3, c. 1 mm long, bifid for half of the length, thin, reflexed. *Fruits* subglobular, 3–3.5 mm in diam, 6-grooved, glabrous, yellow green; pedicel 8–12 mm long, glabrous; columella c. 1 mm long. *Seeds* c. 2 mm high, c. 1 mm wide, smooth, chestnut-brown.

Distribution — Hawai'i (west Maui, O'ahu, Kauai, Molokai and Lanai).

Habitat & Ecology — In dry or rainy forests, thickets and bushland, on rocky ridges, in gulches and on slopes. Altitude: 300–1000 m. Flowering and fruiting the whole year round.

Notes — 1. This species is very variable in leaf shape and size. It can be distinguished by its size and robustness of the branches when compared to other species of subgenus *Macraea*.

2. Sherff (1939) distinguished var. *degeneri* by its distally more alate branchlets and cylindric and more elongate pulvina. None of the distinguishing characters for var. *degeneri* were found in the material. There is a gradient in leaf size, and apex shape that connects var. *distichus* to var. *ellipticus*. Both small- and large-leaved specimens were found on the same islands, which further confirms our decision not to distinguish varieties, but to unite them.

5. **Phyllanthus dumosus** C.B.Rob. — Map 4-5

Phyllanthus dumosus C.B.Rob. (1909) Bot 79; Merr. (1923) 392. — Lectotype (designated here): *FB (M.L. Merritt & F.W. Darling) 13974* (K; iso US), Philippines, Luzon, province of Ilocos Norte.

Shrubs, c. 1 m high, monoecious; much-branched with small branches from main stem; branches light brown, terete, not winged, pubescent when young, otherwise glabrous, side branches often shorter than 5 cm; internodes 0.8–1 mm long. *Stipules* ovate-triangular, c. 0.4 by 0.2 mm, caducous, flat, membranous, margin thinner than center, dark brown when dry, base obtuse, margin entire, apex caudate (tip may break off, then rounded). *Leaves*: petiole 0.2–0.4 mm long, glabrous; blade ovate-orbicular when young, to elliptic, 2–7 by 1.5–3.5 mm, 1.3–2 times longer than wide, membranous, glabrous, base often oblique, slightly cordate, margin not thickened, revolute, apex slightly retuse to rounded, mucronate, upper side often

darker than lower side; midrib slightly raised on lower side, lateral veins 4–6 per side, barely visible. *Staminate flowers* 1 or 2 together, 0.7–0.8 mm in diam; pedicel 1.2–5 mm long, glabrous, slender; sepals 6, red when dry, in two indistinct whorls, obovate, 0.8–1 by 0.8–0.9 mm, apex obtuse or rounded; disc glands 6, flat, slightly ovoid with broad end towards stamen, c. 0.2 by 0.1 mm, c. 0.1 mm high, smooth; stamens 3, c. 0.4 mm long, filaments free, reflexed, thecae rounded to oval, 0.2–0.3 mm long. *Pistillate flowers* usually solitary, c. 1.5 mm in diam when closed, c. 3 mm in diam when opened; pedicel c. 2 mm long, glabrous, slender; sepals 6, in two indistinct whorls, obovate, 0.8–1.2 by c. 0.7 mm, midrib not conspicuous, apex obtuse to acute; disc glands 6, elliptic, partly covered by ovary, only orbicular glands visible, c. 0.3 by 0.1 mm, smooth; ovary sessile, globose, 6-grooved, c. 1 mm in diam, 0.6–0.7 mm high, glabrous; style absent, stigmas 3, 0.3–0.4 mm long, bifid for two third of length. *Fruits* subglobose, 2.5–3.5 mm in diam, 6-grooved, brown when dry, glabrous; pedicel 8–12 mm long; columella c. 1.5 mm long. *Seeds* 1.7 mm long, verrucose-tuberculate along longitudinal lines (Robinson 1909).
Distribution — Philippines (Luzon, Ilocos Norte Prov., Mount Piao).
Habitat & Ecology — Exposed ridges (Robinson 1909). Altitude: c. 1100 m. Flowering and fruiting in November, only known from the type.
Notes — 1. Very similar to *P. chrysanthus*, but differing in the size of the shrub stems and pedicel lengths of the flowers of both sexes.
2. Only the type material is available and this species has not been collected since. The type only contains a few fruits and no seeds. Since the description by Robinson (1909) seems adequate, the species is incorporated here.

6. **Phyllanthus everettii** C.B.Rob. — Map 4-5

Phyllanthus everettii C.B.Rob. (1909) 80; Merr. (1923) 392. — Lectotype (designated here): *FB (Everett) 4301* (K; iso NY, US), Philippines, Negros, Gimagaan river.

Shrubs, up to 3 m high, monoecious; branches terete, flattened in young branches and distal parts of older branches, pubescent; internodes 3–4 mm long. *Stipules* elliptic, 2–3 by 0.8–1 mm, persistent or caducous, membranous, base bilaterally auriculate, margin entire, apex caudate. *Leaves*: petiole 0.5–1 mm, slightly pubescent; blade elliptic to oblong, 11–38 by 4–11 mm, 2.1–3.9 times longer than wide, membranous, glabrous, base obtuse to cuneate, slightly asymmetric, margin not thickened, revolute, apex acute to obtuse, mucronate; midrib slightly raised on both sides, lateral veins 7–11 per side. *Staminate flowers* in fascicles of 2–4, rarely together with a pistillate flower, c. 1.4 mm in diam in bud, c. 2.5 mm in diam when opened; pedicel 2–12 mm long, glabrous; sepals 6, elliptic, slightly ovate, 1.1–1.4 by 0.5–0.8 mm, midrib distinct, but not thickened, apex obtuse, white; disc glands 6, circular to ovate, flat with a non-raised distinct central part, 0.3–0.4 mm in diam, height c. 0.1 mm, smooth; stamens 3, c. 0.8 mm long, filaments free, 0.6–0.8 mm long, anthers c. 0.2 mm high, thecae rounded. *Pistillate flowers* solitary, rarely in pairs, c. 3 mm in diam when open; pedicel 4–24 mm long, glabrous, slender; sepals 6, elliptic to slightly ovate, 1.1–1.5 by 0.8–0.9 mm, midrib conspicuous, apex obtuse; disc entire, 6-lobed, lobes alternating with sepals, c. 1.5 mm in diam, smooth; ovary sessile, subglobose, 6-grooved, 0.7–1 by c. 0.8 mm, tuberculate; style absent, stigmas 3, c. 1 mm long, bifid for two third of length. *Fruits* subglobose, 2.5–3 mm in diam, 6-grooved, glabrous; pedicel 11–25 mm long; columella 1–1.5 mm long. *Seeds* c. 1.4 mm high, c. 1 mm wide, verrucose along longitudinal lines, brown.

Distribution — Philippines (Luzon).

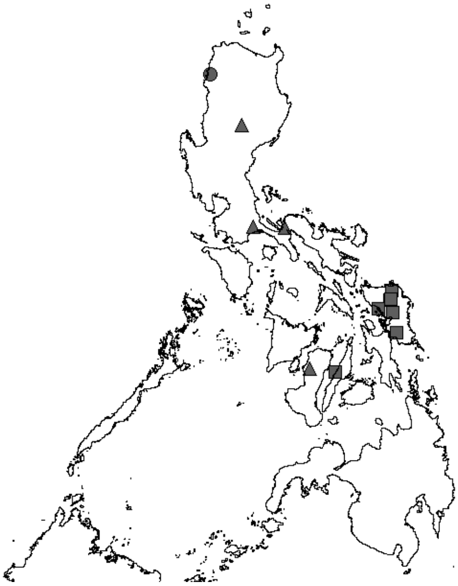
Habitat & Ecology — On forested stream banks at low and medium altitude (Merrill 1923).

Vernacular name — Miagos (Panay Bisáya) (Merrill 1923).

Note — Similar to some of the other species in the Philippines like *P. samarensis* and *P. lancifolius*. This species is distinct by its leaf blades, which are elliptic, as opposed to ovate in *P. lancifolius*, and larger than those found in *P. samarensis*. The resemblance with *P. samarensis* is quite considerable and these species might possibly have to be combined.

7. Phyllanthus exilis S.Moore — Map 4-6

Phyllanthus exilis S.Moore (1926) 97; J.T.Hunter & J.J.Bruhl (1997) 153. — Type:



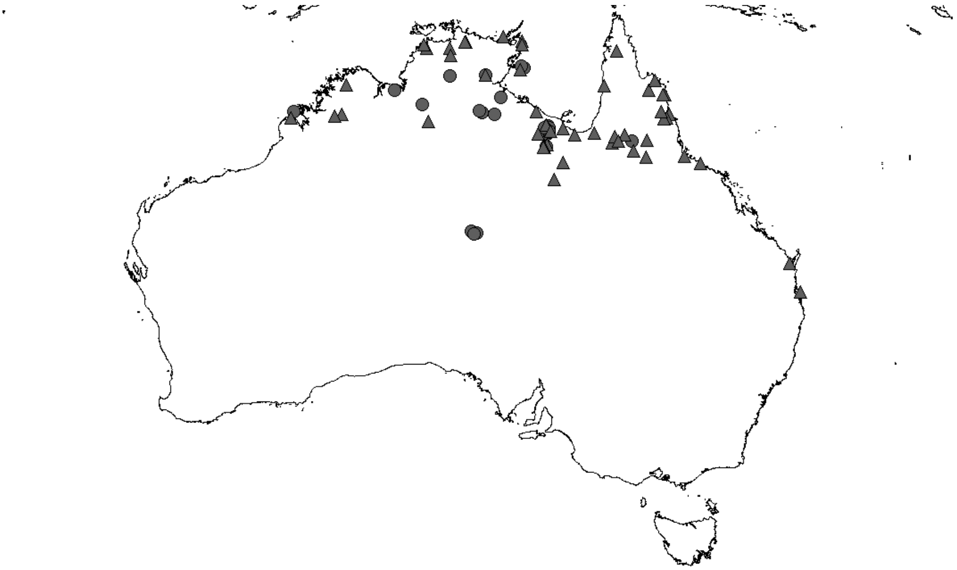
Map 4-5. Distribution of *Phyllanthus dumosus* C.B.Rob. (•), *Phyllanthus everettii* C.B.Rob. (•) and *Phyllanthus samarensis* Müll.Arg. (•) in the Philippines.

G.H. Wilkins 109 (holo K), Australia, Groote Eylandt.

Erect herbs or subshrubs, 30–60 cm tall, monoecious; branches brown, distally slightly flattened and green, glabrous; internodes 2–10 mm long. *Stipules* suborbicular, c. 1 by 0.3 mm, base slightly subcordate, margin entire, apex caudate. *Leaves*: petiole 0.5–1 mm long, glabrous; blade narrowly elliptic, 6–15 by 1–2 mm, 5–7.5 times longer than wide, glabrous, green, base obtuse, rounded or slightly subcordate, margin not thickened, flat, apex obtuse or rounded, often minutely mucronate; midrib sunken above, prominent underneath, lateral veins barely visible, flat above, slightly prominent underneath. *Staminate flowers* solitary to 3 together, c. 0.8 mm in diam; pedicel c. 1 mm long, glabrous; sepals 6, ovate, pale green and reddish, in two whorls, outer ones c. 0.4 by 0.6 mm, apex acute, inner ones c. 0.5 by 0.5 mm, apex obtuse; disc glands 6, circular, c. 0.2 mm in diam, flat, slightly dented in the middle; stamens 3, c. 0.3 mm long, filaments free, reflexed, thecae globular, c. 0.2 mm long. *Pistillate flowers* solitary, c. 1.8 mm in diam; pedicel 2.5–4 mm long, glabrous; sepals 6, ovate, c. 1 by 0.5 mm, pale green and reddish, apex obtuse; disc annular, c. 1 mm in diam, flat; ovary sessile, subglobular, c. 1 mm in diam, c. 0.5 mm high, verrucate; style absent, stigmas 3, c. 0.3 mm long, bifid for half of the length, reflexed. *Fruits* subglobular, c. 2 mm in diam, 6-grooved, basally glabrous, apically minutely verrucate; pedicel c. 5 mm long, glabrous; columella c. 1 mm long. *Seeds* c. 1.5 by 1 mm, smooth, chestnut-brown.
Distribution — Australia (Northern Territory, Queensland and New South Wales).
Habitat & Ecology — In (low) open wood- of shrubland on (shallow) brown or red rocky, loamy, sandy, clayey or skeletal soil. Altitude: 15–385 m. Flowering and fruiting: April to June
Note — Very similar to *P. virgatus*, but with long, extremely narrow leaves. While the ovary of *P. virgatus* can be smooth or verrucate, the ovary of *P. exilis* is always verrucate.

8. Phyllanthus gardnerianus (Wight) Baill. — Map 4-7

Phyllanthus gardnerianus (Wight) Baill. (1858) 628; Thwaites (1861) 282 (as *P. gardneri*); G.L.Webster in Dassan. & Clayton (1997) 212; Chakrab. & N.P.Balakr. (2018) 300. — *Macraea gardneriana* Wight (1852) 27, pl. 1902-3. — *Phyllanthus simplex* Retz. var. *gardnerianus* (Wight) Müll.Arg. (1863) 33; (1866) 392; Hook.f. (1887) 295; N.P.Balakr. & Chakrab. (2007) 381. — *Phyllanthus virgatus* G.Forst. var. *gardnerianus* (Wight) Govaerts & Radcl.-Sm. (1996) 177. — Lectotype (designated by Webster 1997): *G. Gardner s.n.* in *G.H.K. Thwaites C.P. 296* (K), Sri Lanka, Horton Plain.
Phyllanthus miquelianus Müll.Arg. (1863) 33; (1866) 391. —*Diasperus miquelianus* (Müll.Arg.) Kuntze (1891) 600. — Lectotype (designated here): *R.F. Hohenacker 1130A* (G-DC; iso L(L.2247451), India.



Map 4-6. Distribution of *Phyllanthus exilis* S.Moore (•) and *P. minutiflorus* F.Muell. ex Müll.Arg. (•) in Australia.

Phyllanthus patens Miq. ex Müll.Arg. (1863) 34 (non *Phyllanthus patens* Roxb.). — Type: *R.F. Hohenacker 1130* (holo L (L.2248235)) India.

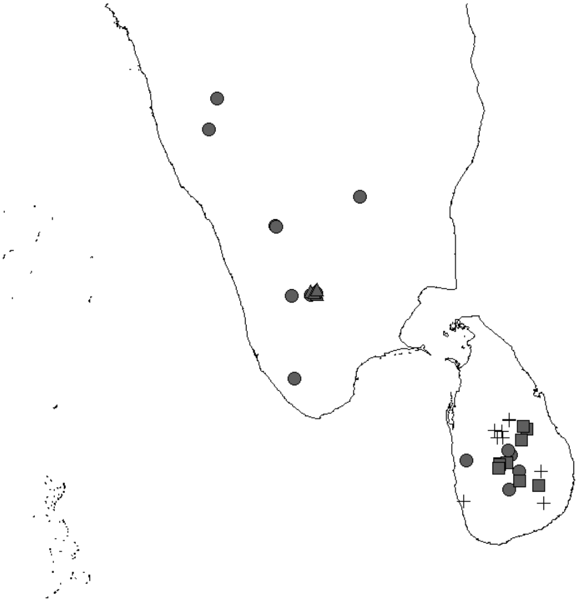
Herbs or subshrubs, sometimes 5–10 cm high, often much higher, monoecious; branches brown, glabrous, distally slightly flattened, often winged; internodes 1–9 mm long. *Stipules* triangular, 1.5–2 by 0.8–1 mm, base cordate, margin entire or erose, apex attenuate. *Leaves*: petiole 0.5–1 mm long, glabrous; blade elliptic, rarely suborbicular, 3–37 by 2.5–18 mm, 1.2–3.5 times longer than wide, glabrous, green above, slightly paler green underneath, base rounded or (sub)cordate, margin not thickened, revolute, apex obtuse or rounded, often minutely mucronate; midrib flat or slightly suppressed above, prominent underneath, lateral veins 3–6 per side, not visible above, slightly prominent underneath. *Staminate flowers* solitary to 12 together, 1.5–2.8 mm in diam; pedicel 2–5 mm long, glabrous, slender; sepals 6, obovate, 1–1.2 by 1–1.2 mm, pink, apex rounded; disc glands 6, circular, flat, c. 0.3 mm in diam; stamens 3, c. 1 mm long, filaments free, reflexed, thecae subovoid, c. 0.2 mm long. *Pistillate flowers* solitary, 4–5.5 mm in diam; pedicel 4–19 mm long, glabrous; sepals 6, elliptic, 1.8–2.4 by 1.4–1.5 mm, red with white margins, apex obtuse; disc annular, flat, slightly crispate, 1.2–1.6 mm in diam; ovary sessile, globular, 1–1.2 mm in diam, 0.8–1 mm high, slightly verrucate; style absent, stigmas 3, 0.8–1.2 mm long, bifid for 4/5 of the length, reflexed. *Fruits* oblate, 2.5–3.8 mm in diam, c. 2 mm high, 6-grooved, with 3 grooves slightly deeper, glabrous or slightly

verrucate; pedicel 4–19 mm long, glabrous; columella c. 1.8 mm long. *Seeds* c. 1.8 by 1.3 mm, smooth, light brown
Distribution — South India and Sri Lanka.
Habitat & Ecology — On rocky montane grasslands and disturbed soils. Altitude: 800–1250 m. Flowering and fruiting: All year round.
Uses —Leaf juice used as eyewash or antiseptic. Fresh leaves, bruised and mixed with buttermilk, used as a cure for children's itch. Root preparations are externally applied to abscesses (Quattrocchi 2016).
Vernacular name — India: Kaattunelli (Quattrocchi 2016).
Notes — 1. Very similar to *P. virgatus*, but with significantly larger pistillate flowers and often with wider leaves.

9. Phyllanthus glaucophyllus Sond. — Map 4-8

Phyllanthus glaucophyllus Sond. (1850) 133; Baill. (1862b) 166; Müll.Arg. (1863) 18 (1866) 393; N.E.Br., Hutch. & Prain (1915) 394; Radcl.-Sm. (1987) 19; Jean F.Brunel (1987) 299, annex 40; M.G.Gilbert (1995) 281; Radcl.-Sm. (1996a) 48; Radcl.-Sm. & Petra Hoffm. (2006) 610. — *Diasperus glaucophyllus* (Sond.) Kuntze (1891) 599. — Lectotype (designated here): *C.L.P. Zeyher 1509* (S; iso MEL), South Africa, Transvaal, Magalisberg.
Phyllanthus glaucophyllus Sond. var. *major* Müll.Arg. (1864) 514; (1866) 393; N.E.Br., Hutch. & Prain in Dyer (1912) 713; Jean F.Brunel (1987) 299. — Lectotype (designated here): *Sanderson 447* (S; iso DBN, K, NH, SAM, TCD), South Africa, Port Natal (currently Durban).
Phyllanthus glaucophyllus Sond. var. *suborbicularis* Hutch. (1920) 395. — Lectotype (designated here): *M.E. Barber 39* (K) South Africa, Kaffranian Mountains.

(Sub)shrubs, 5–100 cm high, monoecious; stems arising from a thick woody rhizome, barely branching; branches winged or minutely ridged, minutely pubescent or glabrous, greyish-green or brown, distally flattened; internodes 3–6 mm long. *Stipules* triangular, 1–2 by 0.3–1 mm, base bilaterally auriculate, margin entire, sometimes denticulate, apex attenuate. *Leaves*: petiole 1–1.5 mm long, glabrous; blade ovate or elliptic, 7–20 by 4–18 mm, 1.1–2.5 times longer than wide, glabrous, base often slightly asymmetrical, (sub)cordate, margin thickened or thin, flat or revolute, apex acute, obtuse or rounded, often minutely mucronate; midrib flat above, prominent underneath, lateral veins 5–7 per side, flat or prominent on both sides. *Staminate flowers* solitary to 5 together, 1.5–2.5 mm in diam; pedicel 2–4 mm long, glabrous, often slender; sepals 6, obovate or elliptic, 1–1.2 by 0.5–1 mm, white, green or yellow, sometimes with white margin, apex rounded; disc glands 6, either circular, flat, c. 0.2 mm in diam or bell-shaped, c. 0.2 mm in diam, 0.2–0.3 mm high; stamens 3, 0.5–1 mm long, filaments free, thecae subglobular, 0.2–0.3 mm long. *Pistillate flowers* solitary, c. 2.5 mm in diam; pedicel 6–10 mm long, glabrous;



Map 4-7. Distribution of *Phyllanthus gardnerianus* (Wight) Baill. (•), *P. macraei* Müll.Arg. (•), *P. myrtifolius* (Moon ex Wight) Müll.Arg. (•) and *P. wheeleri* G.L.Webster (+) in S India and Sri Lanka.

sepals 6, ovate or elliptic, 1–1.5 by 0.5–1 mm, white, green or yellow, apex acute or obtuse; disc annular, slightly lobed, flat, 1.5–2 mm in diam; ovary globular-oblate, 1–1.5 mm in diam, 0.5–1 mm high, glabrous; style absent, stigmas 3, c. 1 mm long, bifid for 2/3–3/4 of the length, reflexed. *Fruits* subglobular, 3–8 mm in diam, 6-grooved, glabrous; pedicel 6–12 mm long, glabrous; columella 1–1.5 mm long. *Seeds* c. 2.5 by 2 mm, verrucate, light brown, verrucae circular, randomly placed or in indistinct longitudinal lines.

Distribution — Southern half of Africa.

Habitat & Ecology — In grasslands, savannahs, woodland, on mountains and slopes, often in rocky areas. Altitude: 100–2000 m. Flowering and fruiting: Whole year round.

Notes — 1. This is the only *Macraea* species that grows from a woody rhizome, and is therefore easily recognizable.

2. Brunel (1987) united *P. glaucophyllus* with *P. alpestris*, but because of the difference in distribution and morphology of the staminate disc glands, we would like to recognize *P. alpestris* as a variety of *P. glaucophyllus*.

3. Another possible synonym of *P. glaucophyllus* might be *P. graminicola* Hutch. because one of the type specimens (*C.F.M. Swynnerton* 261, stored in BM with

barcode BM000911067) was re-identified by Radcliffe-Smith as *P. glaucophyllus*. However, to our knowledge this combination was never published and the description by Hutchinson in Rendle et al. (1911) differs markedly from any species within subgenus *Macraea*. As we have not seen the specimens during this study, we did not include it here.

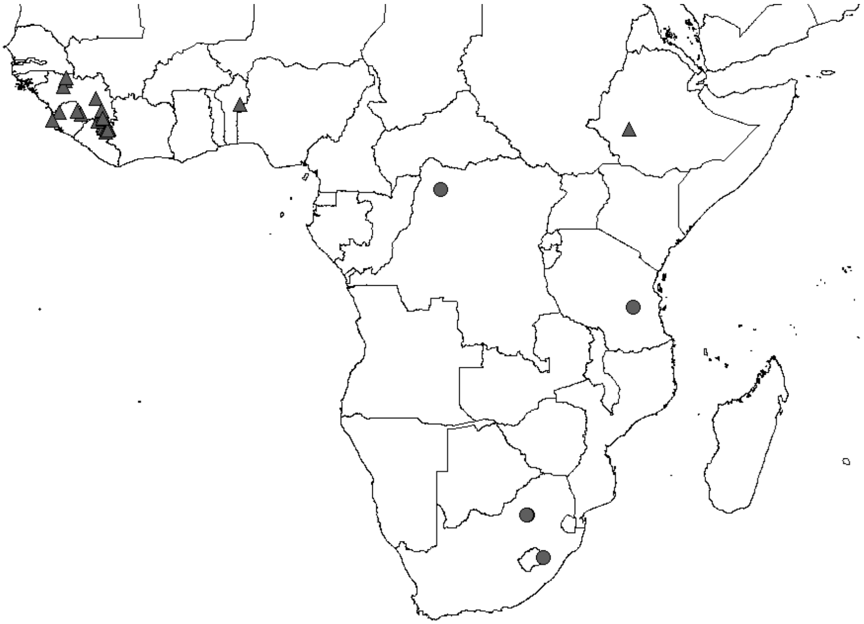
Key to the varieties

1. Leaf blade concolorous. Staminate flowers solitary; disc glands circular, flat. Pistillate pedicels 8–10 mm long. Fruits 3–4 mm in diam .... a. var. *glaucophyllus*
1. Leaf blade discolorous. Staminate flowers 2–5 together; discs glands bell-shaped, 0.2–0.3 mm high. Pistillate pedicels c. 6 mm long. Fruits 6–8 mm in diam... b. var. *alpestris*

a. var. **glaucophyllus**

Phyllanthus glaucophyllus Sond. var. *glaucophyllus*

Subshrubs, 5–30 cm high; branches winged, glabrous, greyish-green; internodes 3–6



Map 4-8. Distribution of *Phyllanthus glaucophyllus* Sond. var. *glaucophyllus* (•) and *P. glaucophyllus* var. *alpestris* (Beille)Verwijs (•) in Africa.

mm long. *Stipules* 1.5–2 by c. 1 mm, base auriculate. *Leaves*: petiole c. 1 mm long; blade 7–20 by 4–18 mm, 1.1–2.5 times longer than wide, concolorous, pale grey-green when dry, base often slightly asymmetrical, cordate, margin thickened, flat, apex acute, obtuse or rounded, minutely mucronate; midrib flat above, prominent underneath, lateral veins 5–7 per side, prominent on both sides, shiny underneath. *Staminate flowers* solitary, c. 2 mm in diam; pedicel c. 4 mm long; sepals obovate, c. 1 by 0.5 mm, white; disc glands circular, flat, c. 0.2 mm in diam; stamens c. 0.5 mm long, thecae c. 0.3 mm long. *Pistillate* pedicel 8–10 mm long, glabrous; sepals ovate, 1–1.5 by c. 1 mm, white, apex acute or obtuse; disc c. 1.5 mm in diam; ovary c. 1 mm in diam, c. 0.5 mm high; stigmas bifid for 2/3 of the length. *Fruits* 3–4 mm in diam; pedicel 8–12 mm long; columella c. 1 mm long. *Seeds* not seen.
Distribution — Southern half of Africa.
Habitat & Ecology — In woodland, and grassy places in forests (Sonder 1850). Altitude: c. 250 m. Flowering and fruiting: unknown.

b. var. **alpestris** (Beille) Verwijs, *comb. et stat. nov.*

Phyllanthus alpestris Beille (1908) 56; N.E.Br., Hutch.& Prain in Dyer (1912) 712; Hutch. & Dalziel (1928) 291; Jean F.Brunel (1987) 299; Essou in Akoègn. et al. (2006) 575. — Type: *A.J.B. Chevalier 12907* (holo P), Guinea, Fouta Djallon.
Phyllanthus leonensis Hutch. (1917) 232; Hutch. & Dalziel (1928) 291. — Type: *N.W. Thomas 580* (holo K), Sierra Leone, Sendugu.
Phyllanthus monticola Hutch. & Dalziel (1928) 291. —Syntypes: *G.F. Scott-Elliot 5819* (K), Sierra Leone, near Regent; *G.F. Scott-Elliot 3962* (K); *C.E. Lane-Poole 424* (K).

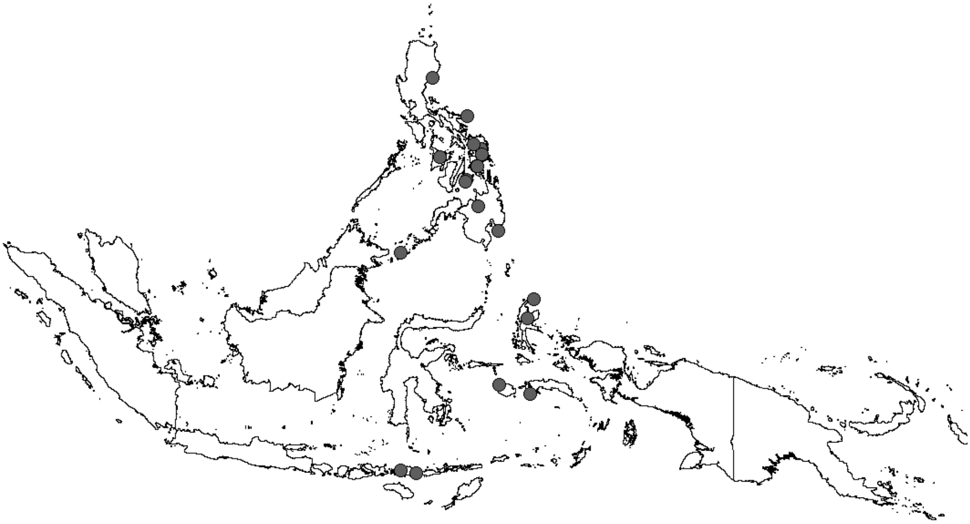
Shrubs, 15–100 cm high; branches minutely ridged, minutely pubescent or glabrous, brown; internodes 6–12 mm long. *Stipules* 1–2 by 0.3–1 mm, base cordate. *Leaves*: petiole 1–1.5 mm long; blade 12–19 by 7.5–13.5 mm, rarely much smaller on the distal branches, 1.4–1.6 times longer than wide, discolorous, upper surface medium to dark green, underneath much paler, base subcordate, margin not thickened, revolute, apex rounded, obtuse or acute; midrib flat above, prominent underneath, lateral veins c. 5 per side, flat above, flat or prominent underneath. *Staminate flowers* 2–5 together, 1.5–2.5 mm in diam; pedicel 2–4 mm long; sepals 6, elliptic, c. 1.2 by 1 mm, green or yellow, sometimes with a white margin; disc glands bell-shaped, c. 0.2 mm in diam, 0.2–0.3 mm high; stamens c. 1 mm long, thecae 0.2–0.3 mm long. *Pistillate* pedicel c. 6 mm long; sepals green or yellow, sometimes with white margin, apex obtuse, in two whorls, outer ones elliptic, c. 1.5 by 0.5 mm, inner ones ovate, c. 1.5 by 1 mm; disc 1.5–2 mm in diam; ovary c. 1.5 mm in diam, c. 1 mm high; stigmas bifid for 3/4 of the length. *Fruits* 6–8 mm in diam, green; pedicel 6–9 mm long; columella c. 1.5 mm long. *Seeds* c. 2.5 by 2 mm, verrucate, light brown, verrucae circular, randomly placed or in indistinct longitudinal lines.

Distribution — Guinea, Liberia, Sierra Leone and Ivory Coast. One specimen was found in Bénin, and one in Ethiopia, the latter is most likely introduced.
Habitat & Ecology — In grasslands, savannahs, on mountains and slopes, often in rocky areas. Altitude: 100–2000 m. Flowering and fruiting: Whole year round.

10. **Phyllanthus lancifolius** Merr.— Map 4-9

Phyllanthus lancifolius Merr. (1914) 489; (1923) 393. — Lectotype (designated here): *BS (M. Ramos) 17465* (US), Philippines, Samar.
Phyllanthus panayensis Merr. (1920) 539; (1923) 394. — Lectotype (designated here): *BS (A. Martelino & G. Edaño) 35655* (US; iso A, K, L (L0016442), P), Philippines, Panay island, Mt. Bulilao.

(Sub)shrubs to trees, 1–8 m high, monoecious or dioecious; branches terete, bark reddish brown, pinkish purplish to light beige, pubescent, young branches with pale spreading short brown hairs; internodes 2–5 mm long. *Stipules* ovate-elliptic, 1.5–2 by 0.6–0.8 mm, caducous, membranous, brown, base bilaterally auriculate, margin entire, apex caudate, acuminate. *Leaves*: petiole 0.3–1 mm, pubescent, brown; blade ovate-elliptic, 9–79 by 3–16 mm, 2–4.6 times longer than wide, membranous, base oblique, rounded, subcordate, margin not thickened, flat, apex acuminate, slightly mucronate, upper side shiny light to dark green or yellowish, lower side pale green, puberulous or glabrous; midrib slightly raised on upper side, sometimes puberulous, lateral veins 8–11 per side, well visible on both sides. *Staminate flowers* several to >10 flowers in axillary fascicles, not all in the same stage, 1–1.6 mm in diam in bud, open 2–3 mm in diam; pedicel 2–12 mm long, glabrous; sepals 6, ovate-elliptic, 1.2–1.6 by 0.6–0.8 mm, greenish to yellowish white, midrib slightly curved inwards and thickened, apex rounded to acute, mucronate; disc glands 6, reniform, 0.1–0.4 mm in diam, c. 0.1 mm high, thin, with a central connective, smooth; stamens 3, 0.5–1 mm long, filaments free, deflexed, thecae rounded, 0.2–0.3 mm long. *Pistillate flowers* solitary or in pairs in usually upper axils, 1.5–2 mm in diam; pedicel 8–50 mm long, glabrous, reddish-purple; sepals 6, whorls indistinct, (ob)ovate to elliptic, 0.8–1.8 by 0.5–0.8 mm, green to yellow or white, midrib not prominent, apex rounded, obtuse or acute; disc annular, slightly cup-shaped and lobed, lobes alternating with sepals, 1.2–1.4 mm in diam, covering ± basal 0.4 mm of ovary, smooth; ovary 3-locular, sessile, depressed subglobose, wider at base, 0.7–1.5 by 0.5–0.6 mm high, each locule with a groove, glabrous or pubescent; style absent, stigmas 3, 0.3–1.2 mm long, bifid for half of length, horizontal or pressed to top of ovary. *Fruits* subglobose, 2.2–3.7 by c. 2 mm, 6-grooved, (pale) green to yellow or white, glabrous or pubescent; pedicel 10–50 mm long; columella 1.2–1.5 mm long. *Seeds* 1.6–1.8 by c. 1.4 mm, brown, minutely verrucate, verrucae circular, along longitudinal lines.
Distribution — Philippines (Bohol, Luzon, Mindanao, Panay, Samar), Lesser Sunda



Map 4-9. Distribution of *Phyllanthus lancifolius* Merr. in Malesia.

Islands (Flores), Moluccas (Ambon, Buru, Dodaga, Morotai).

Habitat & Ecology — On dry slopes or along creeks on limestone or clay soils in secondary forests with dipterocarps. Altitude: 50–100 m.

Notes — 1. Similar to *P. everettii*, but differs in its larger ovate leaves (blades elliptic to oblong, 11–38 by 4–11 mm in *P. everetii*).

2. Listed in Govaerts et al. (2000) as *P. lanceifolius* Merr., but written on the type and in the original publication as *P. lancifolius*.

3. Merrill (1920) described *P. panayensis* as differing from *P. lancifolius* in its smaller leaves and longer pistillate pedicels. However, the leaf size is variable within individuals and specimens were found with leaves of the *P. panayensis* type but with longer pistillate pedicels (e.g., *BS (Ramos) 48249*). As only small differences in proportions were encountered, with overlap between the species, it is logical to merge them.

4. The distribution of this species is greatly expanded with material from the Moluccas and Flores that have typical *Macraea* flowers and seem allied with this species.

11. Phyllanthus macraei Müll.Arg. — Map 4-7

Phyllanthus macraei Müll.Arg. (1863) 29 (non *Phyllanthus rheedii* Wight); (1866) 393; Hook.f. (1887) 296; N.P.Balakr. & Chakrab. (2007) 378; Chakrab. & N.P.Balakr. (2018) 347. — *Macraea rheedii* Wight (1852) 27, pl. 1901. — *Diasperus macraei* (Müll.Arg.) Kuntze (1891) 599 (non *D. rheedei* Kuntze). — Lectotype (designated by Chakrabarty & Balakrishnan 2018): Wight, Icon. Pl. Ind. Orient. 5 (1852) pl. 1901, India, Pulney mountains.

Shrubs, monoecious; branches winged, glabrous or puberulous, dark brown or green, distally flattened; internodes 3–13 mm long. *Stipules* triangular, 1–2 by 0.8–1 mm, base bilaterally auriculate, margin entire, apex attenuate. *Leaves*: petiole 1–2 mm long, glabrous; blade elliptic, 14–45 by 4–18 mm, 1.9–2.8 times longer than wide, glabrous, upper surface medium to dark green, often underneath paler, base cordate, subcordate, rarely rounded, margin not thickened, revolute, often proximally puberulous, apex obtuse or rounded, often mucronate; midrib flat or sunken above, prominent and rarely puberulous underneath, lateral veins 6–9 on each side, flat or sunken above, flat or prominent underneath. *Staminate flowers* 2 or 3 together in axils, c. 4 mm in diam; pedicel 3–6 mm long, glabrous; sepals 6, apex rounded, greenish yellow, in two whorls, outer ones ovate, c. 2 by 1.5 mm, inner ones elliptic, c. 1.5 by 1 mm; disc glands 6, oblate, c. 0.6 mm in diam, c. 0.1 mm high; stamens 3, c. 1 mm long, filaments free, thecae subglobular, c. 0.3 mm long. *Pistillate flowers* solitary, 4–5 mm in diam; pedicel 12–18 mm long, glabrous; sepals 6, apex obtuse or rounded, greenish yellow, in two whorls, outer ones elliptic, c. 2 by 1 mm, inner ones ovate, c. 2 by 2 mm; disc annular, flat, c. 2 mm in diam; ovary sessile, globular, c. 1 mm in diam, c. 1 mm high, verrucate; style absent, stigmas 3, c. 1 mm long, bifid for 3/4 of the length, reflexed. *Fruits* subglobular, 4–5 mm in diam, 6-grooved, glabrous, greenish; pedicel 12–18 mm long, glabrous; columella c. 1.5 mm long. *Seeds* c. 2.5 by 2 mm, smooth or minutely verrucate, dark or chestnut-brown, verrucae circular, randomly and closely placed.

Distribution — South India (Palni hills, Pulney mountains and Kodaikanal).

Habitat & Ecology — Forests and edges of forests near grassland. Altitude: 365–2100 m. Flowering and fruiting: May, June, September, October, December.

Vernacular name— India: Macrae's Leaf-Flower (www.flowersofindia.net).

Notes — 1. Distinguishable by its often puberulous branches and leaf margins.

2. Wight (1852) described this plant as Rheede's *Niruri*, Horti Malab. 10, t. 27 (1690); this drawing is not very detailed, small in scale and lacking staminate flowers and stipules. Wight, Icon. pl. Ind. Orient. 5 Pl. 1901 (1852) is larger scaled, more comprehensive and more precise and therefore more suitable as lectotype.

12. Phyllanthus minutiflorus F.Muell. ex Müll.Arg. — Map 4-6

Phyllanthus minutiflorus F.Muell. ex Müll.Arg. (1865) 75 (non F.Muell. ex Tate, nom. illeg., = *Synostemon trachyspermus* (F.Muell.) I.Telford & Pruesapan); Baill. (1865–1866) 341; Müll.Arg. (1866) 398; Benth. (1873) 112; Airy Shaw (1980) 190; J.T.Hunter & J.J.Bruhl (1997) 158; R.L.Barrett & I.Telford (2015) 158. — *Diasperus minutiflorus* (F.Muell. ex Müll.Arg.) Kuntze (1891) 600. — *Phyllanthus simplex* Retz. var. *minutiflorus* (F.Muell. ex Müll.Arg.) Domin (1927) 877. —*Phyllanthus virgatus* G.Forst. var. *minutiflorus* (F.Muell. ex Müll.Arg.) Airy Shaw (1980) 190, pro syn. — Type: *F.J.H. von Mueller s.n.* (holo G-DC; iso? K), Australia, Northern Territory, Arnhem Land, Victoria River.
Phyllanthus minutiflorus F.Muell. ex Benth. var. *gracillimus* Benth. (1873) 112. — *Phyllanthus simplex* Retz. var. *gracillimus* (F.Muell. ex Benth.) Domin (1927) 877. — Type: *F.J.H. von Mueller s.n.* (holo K), Australia, Queensland Moreton Bay.

Small erect herbs or shrubs, 8–45 cm high, monoecious; branches glabrous, slender, brown or green, minutely ridged, distally flattened and winged; internodes 1–5 mm long. *Stipules* triangular, c. 1 by 0.5 mm, base cordate, margin entire or erose, apex attenuate. *Leaves*: petiole c. 0.5 mm long, glabrous; blade elliptic or ovate, 2–14 by 1–4 mm, 2–5 times longer than wide, glabrous, dark green above, slightly lighter green underneath, base obtuse or rounded, margin not thickened, flat, apex rounded, obtuse or acute; midrib flat or slightly prominent above, prominent underneath, lateral veins not visible. *Staminate flowers* solitary or in pairs with also pistillate flowers, 0.7–1.2 mm in diam; pedicel 0.5–0.8 mm long, glabrous, slender; sepals 6, elliptic, c. 0.4 by 0.2 mm, whitish, apex obtuse; disc glands 6, circular, c. 0.1 mm in diam, flat; stamens 3, c. 0.2 mm long, filaments free, reflexed, thecae ovoid, c. 0.15 mm long. *Pistillate flowers* solitary, rarely in pairs with staminate or pistillate flowers, 1–1.2 mm in diam; pedicel 0.5–2 mm long, glabrous; sepals 6, elliptic, c. 0.5 by 0.3 mm, whitish, apex obtuse, rarely acute; disc annular, flat, slightly crispate, c. 0.4 mm in diam; ovary sessile, globular, c. 0.5 mm in diam, c. 0.4 mm high, glabrous or verrucate; style absent, stigmas 3, c. 0.4 mm long, bifid for half of the length, reflexed. *Fruits* oblate, often splitting into 3 small, blunt tipped valves, 1–1.8 mm in diam, c. 0.8 mm high, 6-grooved, of which 3 slightly deeper than the others, glabrous, green; pedicel 0.5–2 mm long, glabrous; columella c. 0.5 mm long. *Seeds* c. 1 by 0.8 mm, minutely verrucate, light brown, verrucae circular, randomly placed.
Distribution — Australia (Queensland, Northern Territory, Western Australia).
Habitat & Ecology — In (wet) woodlands and swamps. Altitude: 60–825 m. Flowering and fruiting: February to August.
Note — Differing from *P. virgatus* by its slender branches, smaller pistillate flowers on shorter pedicels and smaller fruits and seeds.

13. Phyllanthus myrtifolius (Moon ex Wight) Müll.Arg. — Map 4-7

Phyllanthus myrtifolius (Moon ex Wight) Müll.Arg. (1863) 35; (1866) 396; Thwaites

(1861) 283; Hook.f. (1887) 296; R.Ansari & Jeeja (1993) 141; J.Florence (1997) 134; G.L.Webster in Dassan. & Clayton (1997) 211; Chantar. (2005) 19; in Welzen & Chayam. (2007) 493; N.P.Balakr. & Chakrab. (2007) 379; Chakrab. & N.P.Balakr. (2018) 304. — [*Phyllanthus myrtifolius* Moon (1824) 65, nom nud.; Baill. (1858) 628 (see note 2).] — *Macraea myrtifolia* Moon ex Wight (1852) 27, pl. 1902-2; Baill. (1858) 628. — *Diasperus myrtifolius* (Moon ex Wight) Kuntze (1891) 600. — Lectotype (designated by Webster in Dassanayake & Clayton 1997): *G. Gardner s.n.* in *G.H.K. Thwaites C.P. 650* (K; iso G, PDA), Sri Lanka, Mawelly ganga.

Shrubs, 30–200 cm high, monoecious; branches brown, glabrous, with ridged and fissured bark, distally scabrid and with 2 minute ridges; internodes 2–7 mm long. *Stipules* ovate, 1–2 by 0.8–1 mm, base very narrow, hastate, margin entire, apex acute. *Leaves*: petiole c. 1 mm long, glabrous; blade obovate, 5–25 by 1–10 mm, to 2.5–5.5 times longer than wide, glabrous, upper surface dark green, light green underneath, base very narrow, cordate-sagittate, margin not thickened, (slightly) revolute, apex obtuse or acute; midrib flat above, prominent underneath, lateral veins 4–8 per side, flat above, prominent underneath. *Staminate flowers* solitary to 5 together, c. 2.5 mm in diam; pedicel 5–10 mm long, glabrous, slender; sepals 6, apex obtuse, green or (pinkish) red, often with white margins, in two whorls, outer ones ovate, c. 1.5 by 1 mm, inner ones elliptic, c. 1.5 by 0.5 mm; disc glands 6, ovoid, c. 0.3 by 0.2 mm, c. 0.1 mm high, foveolate; stamens 3, c. 0.5 mm long, filaments free, reflexed, thecae ovoid, 0.2–0.3 mm long. *Pistillate flowers* solitary or in pairs, 2–3 mm in diam; pedicel 6–10 mm long, glabrous, slender; sepals 6, apex obtuse, green or (pinkish) red, often with white margins, in two whorls, outer ones ovate, c. 1.5 by 1 mm, inner ones elliptic, c. 1.5 by 0.5 mm; disc hexagonal with the angles alternating with sepals, flat, c. 1 mm in diam; ovary sessile, globular, c. 0.5 mm in diam, c. 0.5 mm high, glabrous; style absent, stigmas 3, c. 0.5 mm long, bifid for half of the length, reflexed. *Fruits* subglobular, c. 3 mm in diam, 3-grooved, splitting in three blunt tipped valves, glabrous; pedicel 8–10 mm long, glabrous; columella not seen. *Seeds* c. 1.8 by 1.2 mm, smooth or minutely verrucate, chestnut-brown, verruculae rhomboid and stretched widthwise or circular and very small, placed in (indistinct) longitudinal lines.

Distribution — Endemic to Central and South Sri Lanka and cultivated in China, India, Thailand, Singapore, Taiwan, and French Polynesia.

Habitat & Ecology — Common near or even in rivers and on river banks. On granite bedrock and soils with a high water table. Altitude: usually low, up to 900 m. Flowering and fruiting all year -round.

Uses — As an ornamental shrub of hedge, as a medicine for genitourinary infections (Quattrocchi 2016).

Vernacular names — Sri Lanka: Mousetail Plant, Myrtle-leaved leaf-flower (Flowers of India, www.flowersofindia.net), China: Liu xian ye xia zhu (Quattrocchi 2016).

Notes — 1. Similar to *P. samarensis*, but distinguisable by its glabrous branches,

slightly narrower leaves and very narrow cordate-sagittate leaf base.
2. Baillon (1858) treats *Macraea myrtifolia* as part of *Phyllanthus*, but does not make the combination, therefore, according to Art. 35.2 ICN (Turland et al. 2018) the combination *Phyllanthus myrtifolius* cannot be attributed to him.

14. Phyllanthus pacificus Müll.Arg. — Map 4-10

Phyllanthus pacificus Müll.Arg. (*1863) 31;* Drake (1892) 287); (1893) 180; F.Br. *(1935) 137;* J.Florence (1997) 129; W.L.Wagner & Lorence (2011) 82. — *Diasperus pacificus* (Müll.Arg.) Kuntze *(1891) 600.* — *Phyllanthus pacificus* Müll.Arg. var. *typicus* F.Br. (1935) 138, fig. 21h, nom. Inval. — Lectotype (designated by Florence 1997): *E. Jardin 122* (P; iso G-DC), French Polynesia, Marquesas Isl., Noukahiva.
Phyllanthus pacificus Müll.Arg. var. *uapensis* F.Br. *(1935) 138.* — Type: *E.H. Quayle* #X (holo BISH; iso BISH), French Polynesia, Uapou.
Phyllanthus pacificus Müll.Arg. var. *uahukensis* F.Br. *(1935) 139;* St. John (1976) 419. — Lectotype (designated by St. John 1976): *E.P. Mumford & A.M. Adamson 488* (BISH (BISH1001662); iso BISH (BISH1001663)), French Polynesia, Uahuka.
Phyllanthus pacificus Müll.Arg. var. *quaylei* F.Br. *(1935) 139.* — Type: *E.H. Quayle 1341* (holo BISH), French Polynesia, Nukuhiva.

Shrubs, 0.5–2 m high, dioecious, rarely monoecious; branches winged, wings 0.1–0.5 mm wide, dull-brown to red-brown, glabrous, persistent; internodes 5–8 mm long. *Stipules* ovate-triangular, 0.8–2 by 0.5–1.5 mm, caducous, brown, base unilaterally auriculate (or at least more pronounced on side away from leaf), margin scarious, entire, centre slightly thicker, apex rounded. *Leaves*: petiole 0.5–3 mm long, glabrous; blade oblong, ovate, elliptic to suborbicular, 9–61 by 6–19 mm, 1.1–3.7 times longer than wide, subcoriaceous, base rounded to subcordate, cuneate to obtuse, margin not thickened, slightly revolute, apex obtuse to acute, apiculate, upper side dark green, lower side light green, blade sometimes weathering red; midrib sunken above, prominent underneath, lateral veins 4–9 per side, indistinct. *Inflorescences* sometimes on short brachyblasts. *Staminate flowers* up to 8 together, axillary, c. 1.2 mm in diam; pedicel 1.5–2 mm long, glabrous; sepals 6, elliptic, 1.2–1.5 by 1–1.2 mm, greenish-yellowish or white, midrib not prominent, apex rounded; disc glands 6, globose, 0.3–0.5 mm in diam, surface crenulate; stamens 3, 1–1.2 mm long, filaments free, 0.7–0.8 mm long, thecae globose, 0.2–0.4 mm long. *Pistillate flowers* up to 4 together, axillary, 2–3 mm in diam when open; pedicel 3–8 mm long, glabrous, pale to white; sepals elliptic-ovate, 1.2–1.4 by c. 1.1 mm, green-white, midrib not prominent, apex obtuse; disc annular, slightly lobed, lobes alternating with sepals, c. 1.3–1.5 mm in diam, surface crenulate to grooved; ovary sessile, 3-locular, subglobose, c. 0.5 by 0.6–1 mm, each locule with a longitudinal groove, glabrous to minutely tuberculate; style absent, stigmas 3, 0.5–1.0 mm long, 2/3 to completely bifid, horizontal or appressed to ovary. *Fruits* capsular, subglobose, 2.8–3 mm wide by c. 2 mm high, 6-grooved, glabrous, slightly tuberculate, pale to light green; pedicel 3–25 mm long, glabrous, yellowish-green; columella 1.2–1.4 mm long. *Seeds* trigonous, 1.5–2 by 1.2 mm, verrucate, brown, verrucae circular, random or along longitudinal lines.

Distribution — French Polynesia (Marquesas islands: Nuku Hiva, Ua Pou, Fatu Hiva, Hiva Oa, Tahuata).

Habitat & Ecology — Found in forested areas, along streamsides or along windswept ridges of cliffs. Altitude: 25–1200 m. Flowering and fruiting all year round.

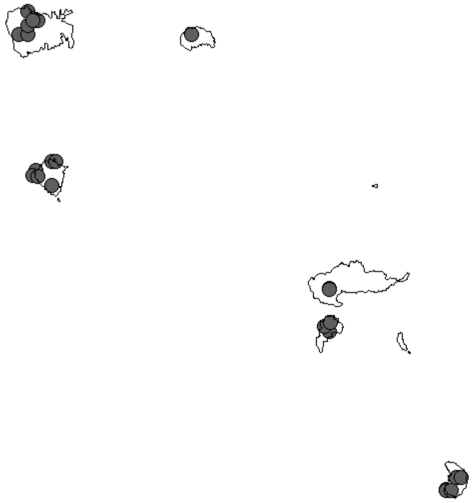
Vernacular names — Marquesas: nouhuu, tia tia; hue iki on Hiva Oa; hueiki, maoo on Nuku Hiva (Florence 1997).

Notes — 1. The placement in subgenus *Macraea* was confirmed by palynological results of Punt (1980).

2. Closely resembles *P. aoraiensis* and *P. urceolatus*, but is mostly different in the size of the leaf blades and the size of the wings.

3. Florence (1997) combined the varieties created by Brown (1935) on the basis of intermediate forms and no real segregation between varieties, even on islands. We agree with this treatment as multiple leaf forms, small to large, can be found on the same island, often with intermediates. There is a slight trend of leaves becoming smaller towards the southern islands, but large forms can still be found there.

15. Phyllanthus prominulatus J.T.Hunter & J.J.Bruhl



Map 4-10. Distribution of *Phyllanthus pacificus* Müll.Arg. in French Polynesia (Marquesas islands).

Phyllanthus prominulatus J.T.Hunter & J.J.Bruhl (1997) 153. — Type: *G.M. Wightman 20* (holo DNA), Australia, Northern Territory, Kalpaga, [precise locality withheld].

Copied from Hunter & Bruhl (1997): Monoecious herb. Branchlets persistent, angular to ellipsoid, slightly winged, 0.6-1.7 cm long, 0.3-0.6 mm wide, glabrous. Stipules persistent, free, 0.5-0.7 mm long, red-brown, ovate to triangular, chartaceous, entire, glabrous; base cordate to amplexicaul; apex acute to acuminate. Branch leaves normal. Branchlet leaves alternate, distichous, jointed, brown when dry or remaining green, symmetrical, plane to concave. Petiole 0.3-0.8 mm long, 0.1-0.4 mm wide, glabrous. Lamina 5-8.8 mm long, 2.4-4.8 mm wide, elliptic, circular to obovate, light-green, paler below, pinnately veined, adaxially prominently veined, abaxially prominulous, glabrous; base symmetrical, rounded to obtuse; apex erect, ecaudate, obtuse to rounded, mucronate; margins plane, thickened; midrib abaxially raised with 4-8 raised parallel lateral veins per side, with marginal loops. Bracts and bracteoles deciduous, glabrous. Inflorescences at least sometimes bisexual with the sexes mixed, indeterminate, axillary, sessile. Male flowers solitary or sometimes clustered, 2-5 per cluster; pedicels 0.4-1.2 mm long, glabrous; sepals 6, free, ascending to divergent, 0.3-0.7 mm long, 0.2-0.5 mm wide, the margins are sometimes lobed once on each side (hastate), white to yellow, elliptic, circular, to ovate, obtuse and acute, glabrous; disk comprising discrete lobes, 0.2-0.4 mm wide, lobes lenticular; stamens 2-3, 1-whorled, erect; filaments free to connate for about half
their length, erect, terete, 0.1-0.3 mm long; anthers extrorse, divaricate, elliptic to circular, 0.1-0.2 mm long. Female flowers solitary or sometimes clustered, 1-2 per cluster; pedicels jointed, at anthesis 0.3-1.1 mm long, 0.1-0.2 mm wide, in fruit 1-2.7 mm long, 0.1-0.2 mm wide, glabrous; sepals free, 6, 0.3-0.5 mm long, 0.2-0.3 mm wide, elliptic to ovate, at anthesis ascending to divergent, in fruit divergent to reflexed, white, green to yellow, with a distinct white margin, obtuse to acute, glabrous; disk crenate, 0.4-0.6 mm wide, glabrous; styles 3, free, divided for half or more of their length, divergent to recurved, yellow to green, 0.2-0.3 mm long, 0.1-0.2 mm wide, narrow-terete, glabrous, branches linear; ovary 0.2-0.5 mm long, 0.3-0.7 mm wide, transversely ellipsoid and apically depressed, smooth, glabrous. Fruit a capsule, septicidal, transversely ellipsoid and apically depressed, 0.8-0.9 mm long, 1.5-1.8 mm wide, yellow-brown, red-brown to green, cartilaginous, smooth, glabrous, grooved septicidally; column persistent, angular-ovoid to 'lanceolate', 0.3-0.5 mm long. Seeds pallid-brown to red-brown, prismatic, laterally compressed, 0.6-0.7 mm long, 0.5-0.7 mm wide, granulate; hilum slightly depressed, circular to ovate, cavity more or less basal.
Distribution — Australia (Northern Territory and Kakadu National Park) (Hunter & Bruhl 1997).
Habitat & Ecology — Occurs in damp parts of savanna woodlands and sedgelands.

Notes — 1. There was insufficient material available to make a description. See Hunter & Bruhl (1997) for a comprehensive description of this species. Distribution and ecological data were taken from Hunter & Bruhl (1997).
2. Distinguished from *P. virgatus* by its lateral veins, which are prominent above, while those of *P. virgatus* are flat above. The veins of both species are slightly prominent underneath.

16. Phyllanthus ridsdalei R.W.Bouman & Verwijs, *sp.nov.* — Fig. 4-1; Map 4-11

Resembling *P. tenuipes* by the presence of a gynophore, but differing in its larger leaves, larger staminate and pistillate sepals, pistillate annular disc (vs free disc glands in the pistillate flowers of *P. tenuipes*) and a longer gynophore and style. The stigmas in *P. ridsdalei* are also only bifid at the tip, while those in *P. tenuipes* are bifid for their entire length. — Type: *C.E. Ridsdale 1479* (holo L (L.3958300); iso A, IBC, K), Philippines, Luzon, Zambales, Santa cruz, Acoje mine concession area, c. N15°46.0' E120°00.0'.

Shrubs, c. 1 m high, monoecious; branches terete, glabrous, slightly winged, wing c. 0.1 mm wide; internodes 6–7 mm long. *Stipules* ovate to elliptic to triangular, c. 1 by 0.3 mm, caducous, flat, membranous, base bilaterally auricled, margin brittle, thin, apex caudate. *Leaves*: petiole 0.8–1.2 mm long, glabrous; blade elliptic, 11–22 by 6–10 mm, 1.5–3.1 times longer than wide, membranous, glabrous, base oblique, subcordate, attenuate to obtuse, margin slightly revolute, apex slightly retuse to acute, upper side darker than lower side; midrib slightly elevated on lower side, lateral veins 5–9 per side, barely visible on upper side. *Staminate flowers* 1–3 together, axillary, 1–1.3 mm in diam; pedicel 10–15 mm long, glabrous; sepals 6, elliptic to oblong, 1.5–2 by 0.8–1 mm, midrib slightly raised on inside of flower, apex curved inward, rounded to obtuse, green turning red; disc glands 6, ovate, 0.5–0.6 by 0.1–0.2 mm, c. 0.3 mm high, massive; stamens 3, c. 1.1 mm long, filaments variably connate from base to more than half of filament length, deflexed, 0.6–0.7 mm long, thecae 0.3–0.4 mm long. *Pistillate flowers* 1 or 2 together, 2.5–3 mm in diam; pedicel 9–13 mm long, glabrous, slender; sepals 6, ovate, c. 3 by 1.5 mm, midrib slightly elevated on inside, apex acute; disc annular, fused with base of gynophore and forming a rim around the base just in front of sepals, rim lobed with lobes alternating with sepals, folded; gynophore 0.6–0.8 mm high, ovary subglobose, 0.4–5 by c. 0.6 mm, each locule with a groove, glabrous, smooth, blueish when dry; style 1.5–1.6 mm long, stigmas 3, 1–2 mm long, with tips bifid, 0.1–0.2 mm long. *Fruits* and *seeds* not seen.
Distribution — Philippines (Luzon).
Habitat & Ecology — Secondary forests on ultrabasic soils. Flowering in May.
Notes — Pollen studied by Wu et al. (2016) showed that this species is part of subgenus *Macraea*, and it was previously filed under 'aff. *samarensis*'. However,

it differs markedly from *P. samarensis* by its larger pistillate flowers, the long gynophore and a long style style below three elongated stigmas.

17. Phyllanthus samarensis Müll.Arg. — Map 4-5

Phyllanthus samarensis Müll.Arg. (1865) 73; (1866) 386; Fern.-Vill. (1880) 188; C.B.Rob. (1909) 79; Merr. (1923) 395; Airy Shaw (1983) 42; Y.J.Chen et al. (2009) 49. — *Diasperus samarensis* (Müll.Arg.) Kuntze (1891) 600. — Type: *Hb. Berol.* (Herb. Berlin) s.n. (B, lost), Philippines, Samar. Neotype (designated here): *BS (M. Ramos) 24460* (neo L; isoneo MO, P), Philippines, Samar, Catubig River.

Shrubs, 50–200 cm high, monoecious; large branches glabrous, with smooth bark, smaller branches tomentellous, distally flattened; internodes 2–5 mm long. *Stipules* triangular, 1.5–2 by c. 1 mm, base auriculate, margin entire, apex attenuate. *Leaves*: petiole c. 1 mm long, mostly glabrous, distally tomentellous on the upper side, rarely entirely tomentellous; blade elliptic, 7–24 by 4–8 mm, 1.8–3 times longer than wide, glabrous, upper surface green, slightly lighter green underneath, base obtuse, margin not thickened, revolute, apex retuse or obtuse, often mucronate; midrib prominent on both sides, lateral veins 8 or 9 on each side, slightly prominent on both sides. *Staminate flowers* 3–7 together, 1.2–2 mm in diam; pedicel 2–10 mm

Map 4-11. Distribution of *Phyllanthus ridsdalei* R.W.Bouman & Verwijs (•) and *Phyllanthus tenuipes* C.B.Rob. (•) in the N Philippines.

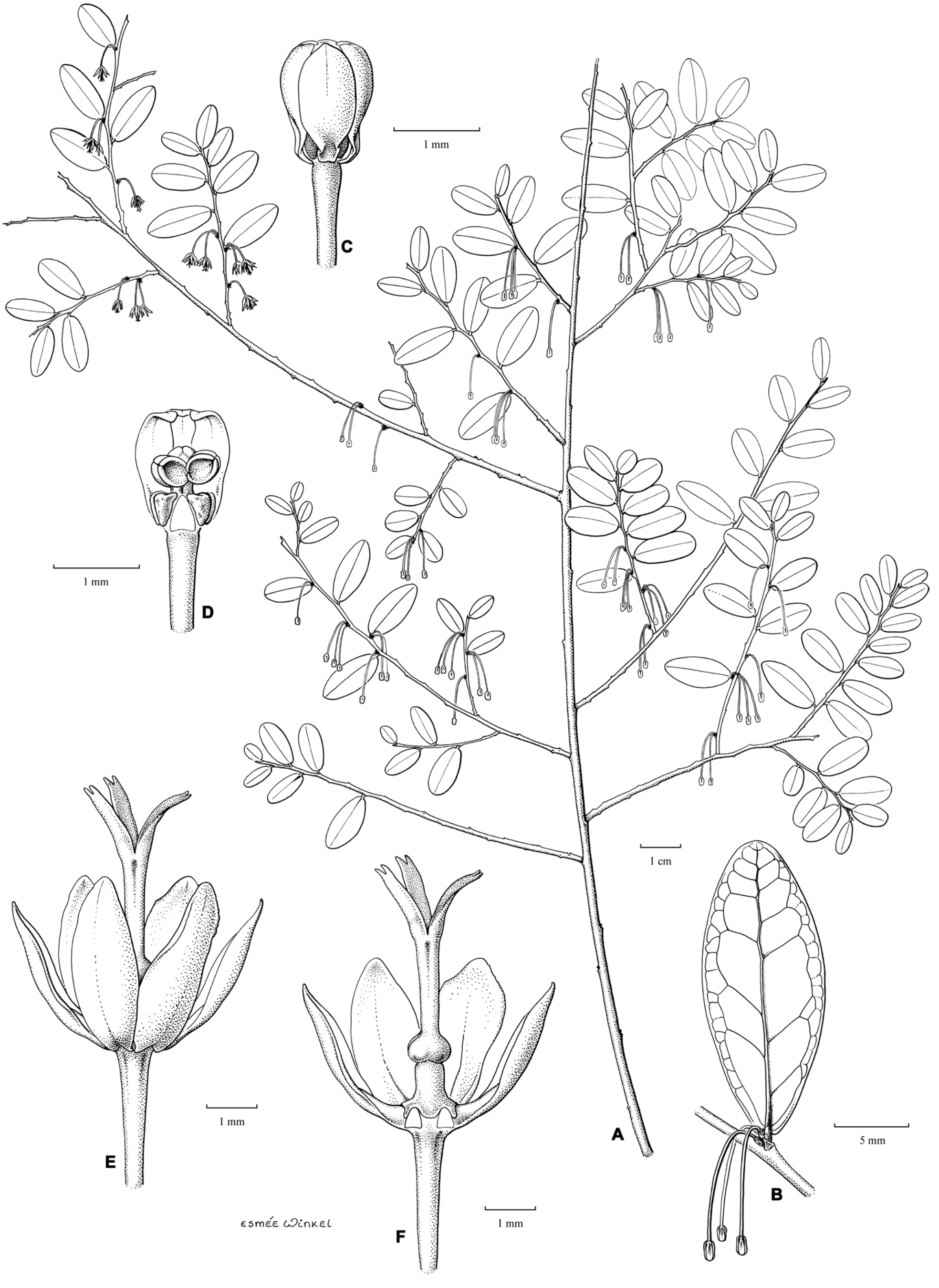


Figure 4-1. *Phyllanthus ridsdalei* R.W.Bouman & Verwijs: A. flowering branch drawn from herbarium specimen with hanging flowers; B. detail of staminate inflorescence; C. closed staminate flower; D. staminate flower (3 sepals removed); E. pistillate flower as seen when open, note the excerted style;

F. pistillate flower (2 sepals removed), note the disc rim fused with the base of the gynophore (all: *C.E. Ridsdale* 1479, L). — Drawing by Esmee Winkel 2018.

long, glabrous, slender; sepals 6, ovoid, c. 0.7 by 1 mm, green or white, apex obtuse; disc glands 6, oblate, c. 0.1 mm in diam, c. 0.05 mm high; stamens 3, c. 0.3 mm long, filaments free, reflexed, thecae ovoid, c. 0.1 mm long; for pollen see Wu et al. (2016). *Pistallate flowers* solitary or in pairs, c. 2.5 mm in diam; pedicel 8–10 mm long, glabrous, base subtomentellous, slender; sepals 6, elliptic, green or white, in two whorls, outer ones c. 1 by 0.7 mm, inner ones c. 1.2 by 0.8 mm, apex obtuse; disc annular, slightly crispate, c. 1.2 mm in diam, flat; ovary sessile, globular, c. 0.8 mm in diam, c. 0.8 mm high, tomentose; style absent, stigmas 3, c. 1 mm long, bifid for 2/3 of the length, robust, reflexed. *Fruits* subglobular, 2.5–3 mm in diam, 6-grooved, bivalved, shortly tomentose; pedicel 8–11 mm long, glabrous, base subtomentellous; columella c. 1 mm long. *Seeds* c. 1.2 by 1 mm, smooth or minutely verrucate along longitudinal lines, chestnut-brown, verrucae very small.
Distribution — Philippines (Samar, Cebu, Leyte).
Habitat & Ecology — Secondary and primary forests, kaigin fields. Brown clay (loam) soil, often over limestone. Altitude: 366–650 m. Flowering and fruiting all year round.
Vernacular name — Malaantagum (Samar-Leyte Bisáya; Merrill 1923).
Note —Similar to *Phyllanthus myrtifolius,* but with densely tomentellous distal branches, slightly wider leaves and obtuse leaf base.

18. Phyllanthus tararae Verwijs *stat. & nom nov.* — Map 4-8

Phyllanthus virgatus G.Forst. var. *hirtellus* Airy Shaw (1980) 195 (non *P. hirtellus* F.Muell. ex Müll.Arg.). — Type: *L.J. Brass 8651* (holo K; iso L (L0016455)), Papua New Guinea, Western Division, Wassi Kussa River, Tarara.

Erect shrubs, c. 100 cm high; branches brown, densely whitish hirtellous, minutely ridged, distally slightly flattened and winged; internodes 1.1–2.8 mm long. *Stipules* triangular, 2–2.5 by c. 1 mm, base cordate, margin entire or erose, apex attenuate. *Leaves*: petiole c. 0.5 mm long, whitish hirtellous or glabrous; blade elliptic, 7–14 by 2–4 mm, 3.2–4.7 times longer than wide, densely whitish hirtellous on both sides, dark green above, slightly lighter green underneath, base rounded, margin not thickened, slightly revolute, apex acute, mucronate; midrib flat or sunken above, prominent underneath, lateral veins not visible. *Staminate flowers* solitary or in pairs, 0.7–1.2 mm in diam; pedicel 4–5 mm long, glabrous, slender; sepals 6, elliptic, c. 1 by 0.7 mm, apex obtuse; disc glands 6, circular, c. 0.3 mm in diam, flat; stamens 3, c. 0.4 mm long, filaments free, slightly reflexed, thecae ovoid, c. 0.15 mm long. *Pistillate flowers* solitary, c. 3.5 mm in diam; pedicel 2–11 mm long, whitish hirtellous, rarely glabrous; sepals 6, elliptic, 0.8–1.4 by 0.3–0.5 mm, apex obtuse; disc annular, slightly crispate, c. 1 mm in diam, flat; ovary sessile, globular, 0.8–1.2 mm in diam, 0.5–0.8 mm high, whitish hirtellous or glabrous; style absent, stigmas 3, c. 0.8 mm long, bifid for 2/3 of the length, reflexed. *Fruits* oblate, c. 3 mm in diam, c. 2 mm high, 6-grooved, whitish hirtellous or glabrous; pedicel 5–11 mm long, densely whitish hirtellous, rarely glabrous; columella c. 1 mm long. *Seeds* c. 1.2 by 1 mm, minutely verrucate, chestnut-brown, verrucae circular, randomly placed or in indistinct longitudinal lines.

Distribution — Papua New Guinea (Western Province).

Habitat & Ecology — In grassland and savannah forests. Flowering and fruiting likely all year round.

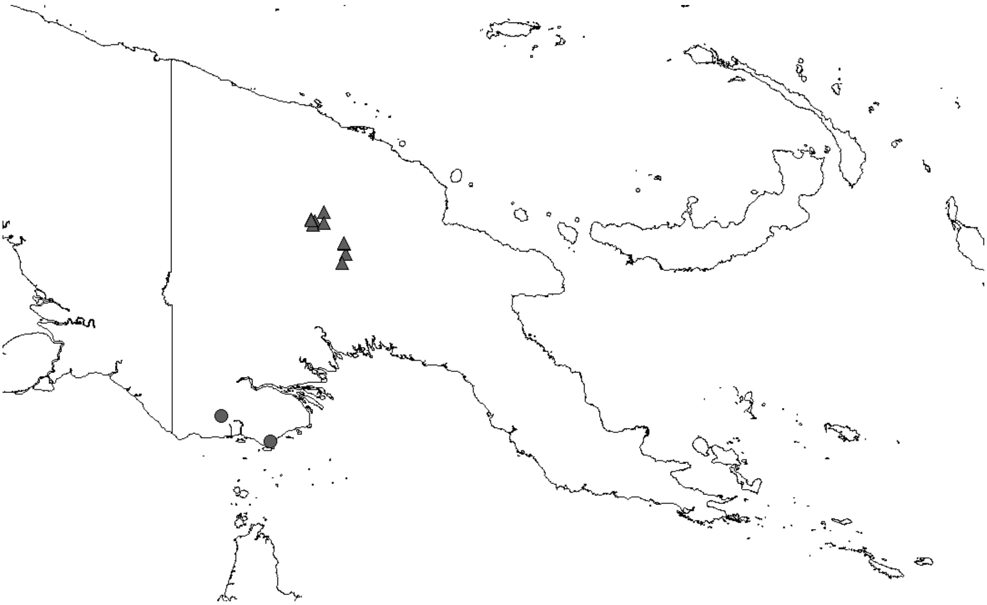
Notes — 1. Can be distinguished from *P. virgatus* and *P. chrysanthus* var. *chrysanthus* by its densely hirtellous branches and leaves and from *P. chrysanthus* var. *deverdensis* and var. *micrantheoides* by its hirtellous leaves with acute apex. The leaves of *P. tararae* are larger than those of *P. chrysanthus* var. *deverdensis* and narrower than those of *P. chrysanthus* var. *micrantheoides*.

2. Only two specimens were seen, both from Papua New Guinea. No other comparable specimens with similar leaves and pubescence were found.

19. Phyllanthus tenuipes C.B.Rob. — Map 4-11

Phyllanthus tenuipes C.B.Rob. (1909) 78; Merr. (1923) 396. — Lectotype (designated here): *E.D. Merrill 4419* (K; iso US, NY), Philippines, Luzon, Benguet.

Shrubs to trees, up to 15 m high, monoecious, dbh at least 15 cm; branches terete, slightly winged, wings c. 0.1 mm wide, branches covered with short stiff brown hairs; internodes 2–4 mm long. Outer *bark* brown, inner bark reddish, sometimes with yellow sap. *Stipules* ovate to triangular, c. 1.2 by 0.5–0.6 mm, caducous or persistent, membranous, base bilaterally auriculate, margin brittle, thin, entire, apex acute. *Leaves*: petiole 0.4–0.8 mm long, puberulous; blade elliptic to ovate, orbicular in earliest leaves on side branches, 5–14 by 2.5–10 mm, 1.1–2.4 times longer than wide, membranous, glabrous, base truncate to rounded to obtuse, sometimes subcordate, margin slightly revolute, apex rounded to obtuse to acute, mucronate, upper side lighter than lower side; midrib barely elevated on lower side, lateral veins 5–7 per side. *Staminate flowers* solitary, 0.6–0.8 mm in diam; pedicel 2–24 mm long, glabrous, slender; sepals 6, oblong, 1–1.1 by c. 0.5 mm, reddish with white margin, midrib not elevated, apex rounded; disc glands 6, ovate, 0.3–0.4 mm long, c. 0.2 mm high and wide, smooth; stamens 3, c. 0.5 mm long, filaments free,



Map 4-12. Distribution of *Phyllanthus tararae* Verwijs (•) and *P. womersleyi* Airy Shaw & G.L.Webster (•) in Papua New Guinea.

deflexed to horizontal position, thecae globose, c. 0.2 mm long, rounded. *Pistillate flowers* solitary or in pairs, axillary, 1.2–1.5 mm in diam; pedicel c. 18 mm long, glabrous, slender; sepals 6, oblong to ovate, 1.3–1.8 by 1–1.1 mm, apex rounded or slightly obtuse; disc glands 6, circular, c. 0.3 mm in diam by c. 0.1 mm high, crumpled; ovary on short gynophore of c. 0.1 mm, subglobose, 6-grooved, glabrous, smooth; style 0.3–0.6 mm long, stigmas 3, 0.2–0.5 mm long, completely bifid. *Fruits* depressed globose, 1.5–2.5 mm in diam, c. 1.5 mm high, 6-grooved, brown, glabrous, smooth; pedicel 15–21 mm long; columella without gynophore c. 0.9 mm long, width c. 1.5 mm. Seeds trigonous, 1.1–1.2 by c. 1 mm, brown, minutely verrucate along longitudinal lines.

Distribution — Philippines (Luzon (Benguet), Daklan to Kabayan, Itogon to Dilopirop).

Habitat & Ecology — In primary or secondary forests along cliffs or roadsides, sometimes on ultrabasic soils. Altitude: 50–1500 m. Flowering and fruiting all year round.

Note — Described by Robinson (1909) as an undershrub of 30 cm high, but other specimens are shrubs of 1.5 m to trees of 15 m. Two main forms can be distinguished. The original, as described by Robinson, and a tree form with yellow sap and diamond-shaped leaves (*C.E. Ridsdale ISU 276*).

20. Phyllanthus urceolatus Baill. — Map 4-2

Phyllanthus urceolatus Baill. (1862a) 239 (non Noronha, 1790, nom. nud.); Müll. Arg. (1866) 386; Drake (1893) 180; Guillaumin (1948) 176; M.Schmid (1991) 44; J.Florence (1997) 129. — *Diasperus urceolatus* (Baill.) Kuntze (1862) 601. — *Phyllanthus pinaiensis* S.L.Welsh (1998) 112; W.L.Wagner & Lorence (2011) 83, nom. superfl. — Lectotype (designated here)*: E. Vieillard 336* (P (P00066432); iso P(P00066433)), French Polynesia, Port de France.

Shrubs, 40–150 cm high, monoecious; branches dark brown, glabrous, distally slightly flattened, not winged or ridged, sometimes green; internodes 3–15 mm long. *Stipules* ovate, c. 0.5 by 0.5 mm, base cordate, margin entire or (extremely) erose, apex acute. *Leaves*: petiole 1–4 mm long, glabrous; blade elliptic or ovate, 22–85 by 10–40 mm, 1.4–3.6 times longer than wide, glabrous, green, base cuneate or attenuate, rarely rounded, margin not thickened, flat, apex narrow and obtuse, rarely rounded, minutely mucronate; midrib prominent on both sides, lateral veins 10–18 per side, prominent on both sides. *Staminate flowers* solitary to 3 together, c. 1.5 mm in diam; pedicel c. 6 mm long, glabrous; sepals 6, elliptic, 0.6–0.8 by c. 0.6 mm, greenish, reddish, red or purple, apex obtuse; disc glands 6, circular, flat, c. 0.3 mm in diam; stamens 3, c. 0.6 mm long, robust, filaments free, reflexed, thecae globular, c. 0.1 mm long. *Pistillate flowers* solitary, c. 3 mm in diam; pedicel 10–30 mm long, glabrous; sepals 6, elliptic, 1–1.2 by c. 0.8 mm, greenish, apex obtuse, red or purple; disc annular, flat, c. 1 mm in diam; ovary sessile, globular, c. 1 mm in diam, c. 0.8 mm high, glabrous; style absent, stigmas 3, c. 0.9 mm long, bifid for 3/4 of the length, slender, reflexed. *Fruits* subglobular, 2.5–4 mm in diam, 6-grooved, glabrous, green or red; pedicel 10–30 mm long, glabrous; columella c. 1.5 mm long. *Seeds* c. 2.5 by 1.5 mm, (light) brown, minutely verrucate, verrucae circular, randomly placed or longitudinally linear.
Distribution — French Polynesia (Tahiti, Moorea, Ra'iātea).
Habitat & Ecology — In (mesophilic) forest, on crests and slopes. Altitude: 224–830 m. Flowering and fruiting all year round.
Vernacular name — Tahiti: E vou (*M.J. Lepiné s.n.*)
Note — Recognisable by its large leaves with long pedicels.

21. Phyllanthus ussuriensis Rupr. & Maxim. — Map 4-14

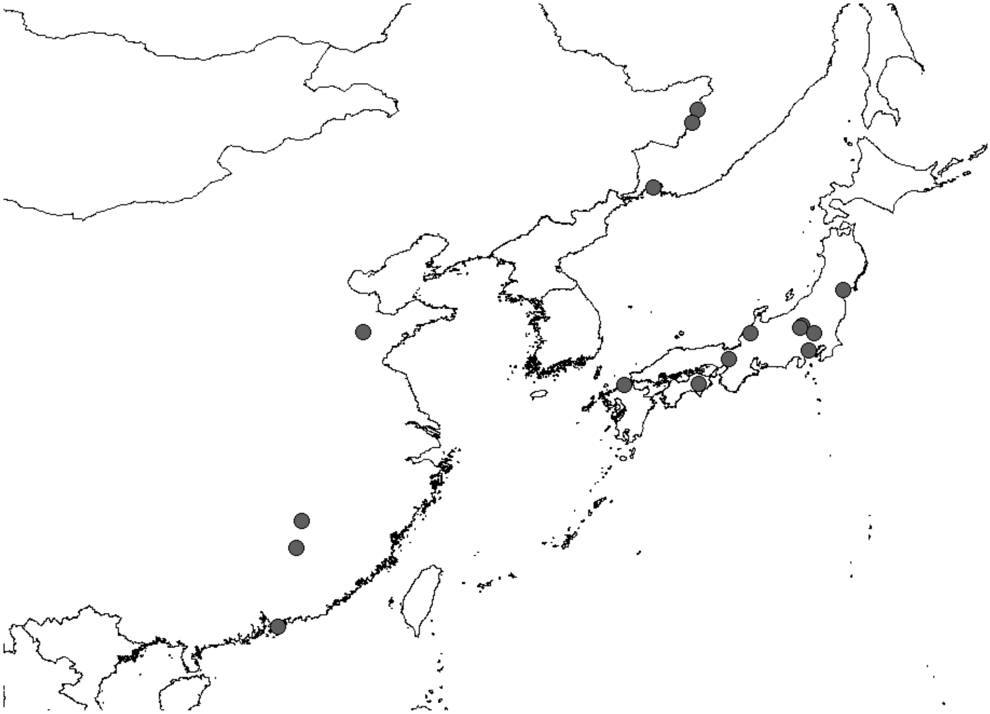
Phyllanthus ussuriensis Rupr. & Maxim. (1857) 222; P.T.Li & M.G.Gilbert in Z.Y.Wu, P.H.Raven & D.Y.Hong (2008) 182. — *Phyllanthus anceps* Benth. (1861) 311, nom. illeg., non *Phyllanthus anceps* Vahl; F.B.Forbes & Hemsl. (1894) 420. —*Phyllanthus simplex* Retz. var. *ussuriensis* (Rupr. & Maxim.) Müll.Arg. (1863) 33; (1866) 392. — *Phyllanthus wilfordii* Croizat & F.P.Metcalf (1942) 194, nom. superfl. — Type: *C.J. Maximowicz s.n.* (holo probably LE; iso K, M, NY), Russia, Ussuri.
Phyllanthus simplex Retz. var. *chinensis* Müll.Arg. (1863) 33; (1866) 391. —

Phyllanthus virgatus G.Forst. var. *chinensis* (Müll.Arg.) G.L.Webster in E.Walker (1971) 68. — Syntypes: *Park 57* (G-DC), China, Canton; *Hance 1223* (B, presumably lost), China, Hongkong; *C. Wilford 66* (A), China, Hongkong.
Phyllanthus matsumurae Hayata ex Yabe (1904) 12. — Type: Not designated.

Erect herbs, 10–45 cm high, monoecious; branches brown, glabrous, minutely ridged, distally flattened and winged; internodes 3–13 mm long. *Stipules* triangular, 1–1.2 by 0.5–0.8 mm, base cordate, margin entire or serrate, apex attenuate. *Leaves*: petiole c. 0.5 mm long, glabrous; blade elliptic, 4–25 by 1.5–8 mm, 2.4–5 times longer than wide, glabrous, green, base obtuse, rounded or minutely cordate, sometimes slightly asymmetrical, margin not thickened, slightly revolute, apex obtuse or acute, rarely rounded; midrib prominent on both sides, lateral veins 4–9 per side, prominent on both sides. *Staminate flowers* solitary to 3 together, 0.8–1 mm in diam; pedicel c. 1 mm long, glabrous, slender; sepals 4 or 6, ovate or oblong, c. 0.4 by 0.2 mm, apex rounded; disc glands 4 or 6, cupuliform, c. 0.1 mm in diam, c. 0.1 mm high; stamens 2 or 3 (often on the same plant), c. 0.4 mm long, filaments free, reflexed, thecae ovoid, c. 0.2 mm long. *Pistillate flowers* with 1 or 2 staminate flowers, rarely solitary, c. 1 mm in diam; pedicel c. 1 mm long, glabrous; sepals 6, ovate, 0.3–0.8 by c. 0.2 mm, apex rounded; disc glands 6, alternate, protruding from between the sepals, ovate or oblong, 0.15–0.2 by c. 0.1 mm, flat; ovary sessile, globular, c. 0.8 mm in diam, c. 0.5 mm high, glabrous or verrucate; style very short, stigmas 3, c. 0.3 mm long, bifid for half of the length, reflexed. *Fruits* subglobular, 2–2.5 mm in diam, 6-grooved, sometimes bivalved, glabrous or verrucate; pedicel 2–3.5 mm long, glabrous; stigmas, sepals and disc glands persistent; columella c. 1 mm long. *Seeds* c. 1 by 1 mm, smooth or minutely verrucate, dark or chestnut-brown, verrucae small, very prominent and randomly placed.
Distribution — Southeast Russia, China, Japan.
Habitat & Ecology — Near rivers and ponds, in moist places under woods. Altitude: 45–630 m. Flowerering: June to October.
Uses — All parts are used as an astringent or antidiarrheal (Li & Gilbert 2008; Quattrochi 2016).
Vernacular names — China: Mi gan cao (蜜柑草), Sweet orange grass (Chinese, mandarin, Li & Gilbert 2008).
Notes — This is the only species in subgen. *Macraea* with staminate flowers with 4 sepals, 2 stamens and 4 disc glands, though staminate flowers with 6 sepals, 3 stamens and 6 disc glands also occur, often on the same plant. The 6 disc glands of the pistillate flowers, while not a unique character, distinguish this species from the vegetavively very similar *P. virgatus*, which has an annular disc in its pistillate flowers.

22. Phyllanthus virgatus G.Forst. — Map 4-15

Phyllanthus virgatus G.Forst. (1786) 65; Hook. & Arn. (1826) 69; G.L.Webster & Airy Shaw (1971) 86; Airy Shaw (1975) 186; (1980) 194; Punt (1980) 163; A.C.Sm. (1981) 464; G.L.Webster (1986) 94; Lobr.-Callen et al. (1988) 294; J.T.Hunter & J.J.Bruhl (1997) 157; M.Schmid (1991) 44; Chantar. in Welzen & Chayam. (2007) 504; P.T.Li & M.G.Gilbert in Z.Y.Wu, P.H.Raven & D.Y.Hong (2008) 181; Y.J.Chen et al. (2009) 49; R.L.Barrett & I.Telford (2015) 158. — *Phyllanthus simplex* Retz. var. *virgatus* (G.Forst.) Müll.Arg. (1863) 32; (1866) 392. — *Diasperus virgatus* (G.Forst.) Kuntze (1891) 597. — Lectotype (designated by A.C.Smith 1981): *Banks & Solander s.n.* (holo BM), Tahiti.
Phyllanthus simplex Retz. (1789) 29; Thwaites (1861) 282; Baill. (1862a) 237; Müll. Arg. (1863) 32; (1866) 391; Laness. (1866) 611; Miq. (1867) 127; Benth. (1873) 111; Hook.f. (1887) 295; Drake (1893) 181; F.B.Forbes & Hems. (1889-1902) 423; C.B.Rob. (1909) 81; Merr. (1923) 395; Domin (1927) 876; Guillaumin (1948) 177; J.T.Hunter & J.J.Bruhl (1997) 157; G.L.Webster in Dassan. & Clayton (1997) 213; W.J.Kress et al. (2003) 234; N.P.Balakr. & Chakrab. (2007) 38; Chakrab. & N.P.Balakr. (2018) 307.— *Phyllanthus simplex* Retz. var. *genuinus* Müll.Arg. (1866) 391, nom. inval.; Domin (1927) 877. — Type: *Koenig s.n.* (holo C) India, Tranqebar.
Phyllanthus anceps Vahl (1791) 95. — *Melanthesa anceps* (Vahl) Miq. (1859) 371. — Type*: Unknown collector s.n.* (holo C).



Map 4-13. Distribution of *Phyllanthus ussuriensis* Rupr. & Maxim. in East Asia.

Phyllanthus pedunculatus Kostel. (1836) 1769. — *Phyllanthus depressus* Buch.-Ham. ex Dillwyn (1839) 51, nom. illeg., nom. superfl.; Müll.Arg. (1866) 432. —*Diasperus pedunculatus* (Kostel.) Kuntze (1891) 597. —*Diasperus depressus* Kuntze (1891) 599, nom. Illeg., nom. superfl. — Type: *Rheede,* Horti Malab. 10 (1690) t. 27.
(*Phyllanthus fruticosus* B.Heyne ex Benth. in Wall., Numer. List (1847) 237 (nr. 7899A), nom. nud.)
(*Phyllanthus marginatus* B.Heyne ex Benth. in Wall., Numer. List (1847) 237 (nr. 7899A), nom. nud.)
Macraea oblongifolia Wight (1852) 27, pl. 1902-1. — Lectotype (designated by G.L.Webster in Dassan. & Clayton 1997): Wight, Icon. Pl. Ind. Orient. 5 (1852) pl. 1902-1.
Macraea ovalifolia Wight (1852) 27, pl. 1902-4. — Lectotype (designated here): Wight, Icon. Pl. Ind. Orient. 5 (1852) pl. 1902-4.
Melanthesa rupestris Miq. (1859) 371. — Type: *Zollinger s.n.* (holo U (U0002059); iso P, PC), Indonesia, Flores.
Phyllanthus pratensis Pancher ex Baill. (1862a) 237. — *Phyllanthus simplex* Retz. var. *pratensis* (Pancher ex Baill.) Müll.Arg. (1863) 33; (1866) 392. — Type: *E. Vieillard 1197*, 1855 (holo P (P00066448); iso G-DC (G00318230), P (P00066449, P00066450, P00066451)), New Caledonia, Saint-Vincent.
Phyllanthus conterminus Müll.Arg. (1863) 32; (1866) 389. —*Diasperus conterminus* (Müll.Arg.) Kuntze (1891) 599. — Type: *Hogdson 215* (holo G-DC (G00325912)), Australia.
Phyllanthus simplex Retz. var. *myriocladus* Müll.Arg. (1863) 33; (1866) 392. — Type: *E. Vieillard 1199* (holo G-DC (G00318219); iso P (P00066447)), New Caledonia, Fort de France.
Phyllanthus beckleri Müll.Arg. (1865) 74; Baill. (1865-1866) 341; (1866) 390; J.T.Hunter & J.J.Bruhl (1997) 157. — *Diasperus beckleri* (Müll.Arg.) Kuntze (1891) 598. — Type: *H. Beckler 668* (holo G-DC (G00319824)), Australia, Clarence river.
Phyllanthus simplex Retz. var. *brevipes* Müll.Arg. (1866) 392. — Type: *E. Viellard s.n.* (holo G-DC; iso? P (P00066452 & P00066453)), New Caledonia, Wagap.
Phyllanthus filicaulis Benth. (1873) 111; J.T.Hunter & J.J.Bruhl (1997) 157. — *Phyllanthus simplex* Retz. var. *filicaulis* (Benth.) Domin (1927) 876. — Type: *C. Stuart s.n.* (holo K), Australia, New South Wales, New England.
Phyllanthus simplex Retz. var. *leiospermus* Benth. (1873) 111. —*Phyllanthus simplex* Retz. var. *genuinus* subvar. *leiospermus* (Benth.) Domin (1927) 876, nom. inval. — Type: *T.L. Mitchell 66* (holo K), Australia, Narren river.
Phyllanthus trachygyne Benth. (1873) 103; J.T.Hunter & J.J.Bruhl (1997) 157. — Lectotype (designated by J.T.Hunter & J.J.Bruhl 1997): *M. Schultz 668* (K), Australia, Northern Territory, Port Darwin.
Phyllanthus weinlandii K.Schum. in K.Schum. & Lauterb. (1905) 287. —Syntypes: *K. Weinland 241* (BRI, K, M), Papua New Guinea, Morobe Province, Finschhafen; *K. Weinland 389a* (n.v.), Papua New Guinea, Matatakum.

Phyllanthus eboracensis S.Moore (1920) 216; J.T.Hunter & J.J.Bruhl (1997) 158. — Type: *E. Dämel s.n.* (holo BM, not seen; iso K), Australia, Cape York.
Phyllanthus narayanswamii Gamble (1925a) 329; (1925b) 1290; N.P.Balakr. & Chakrab. (2007) 381; Chakrab. & N.P.Balakr. (2018) 349. — Lectotype (designated by Chakrabarty & Balakrishnan 2018): *V. Narayanswami* 640 (K; iso CAL, not seen), India, Dummakouda, Rampa hills, Godawari district.
Phyllanthus simplex Retz. var. *myrtifolius* Domin (1927) 876; J.T.Hunter & J.J.Bruhl (1997) 158. — Type: *Domin s.n.* (n.v.), Australia, North East Queensland.
Phyllanthus simplex Retz. var. *pinifolius* Domin (1927) 877; J.T.Hunter & J.J.Bruhl (1997) 158. — Type: *Domin s.n.* (n.v.), Australia, Queensland.

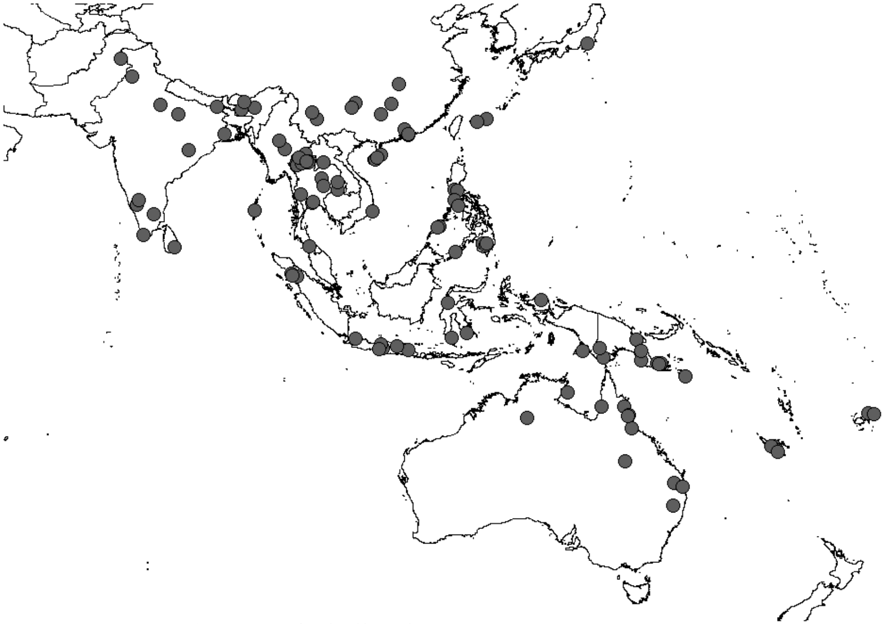
Usually erect, rarely sprawling shrubs or herbs, 30–100 cm high, monoecious; branches brown or purplish, minutely ridged, glabrous, distally brown or sage-green, flattened and winged; internodes 1–5 mm long. *Stipules* triangular, 1–2.5 by 0.5–1 mm, base cordate, margin entire or erose, apex attenuate. *Leaves*: petiole 0.5–1 mm long, glabrous; blade elliptic or ovate, rarely suborbicular or obovate, 3–40 by 1–6 mm, (1–)2.5–5(–6.7) times longer than wide, glabrous, dark green above, lighter green underneath, base rounded, margin not thickened, (slightly) revolute, rarely flat, apex acute, obtuse or rounded, often minutely mucronate; midrib flat above, prominent underneath, lateral veins 5–8 per side, flat above, slightly prominent underneath. *Staminate flowers* solitary or in pairs with sometimes a pistillate flower, 0.8–1.7 mm in diam; pedicel 0.2–5 mm long, glabrous, slender; sepals 6, elliptic, 0.5–1 by 0.2–0.5 mm, red to purple to green to yellow to white, apex obtuse; disc glands 6, circular, c. 0.2 mm in diam; stamens 3, c. 0.4 mm long, filaments free, reflexed, thecae ovoid, c. 0.2 mm long; for pollen see Punt (1980) and Wu et al. (2016). *Pistillate flowers* solitary, rarely in pairs, with sometimes a staminate flowers, 1.5–2.6 mm in diam; pedicel 3–9 mm long, glabrous; sepals 6, elliptic, 0.8–1.2 by 0.3–0.5 mm, red to purple to green to yellow to white, apex obtuse, rarely acute; disc annular, slightly crispate, flat, c. 0.9 mm in diam; ovary sessile, globular, c. 0.8 mm in diam, c. 0.5 mm high, glabrous or verrucate; style absent, stigmas 3, c. 0.6 mm long, bifid for half of the length, reflexed. *Fruits* oblate or subglobular, often bivalved, 2–3.5 by 1.5–2 mm, 6-grooved, of which often 3 slightly deeper, greenish, glabrous or verrucate; pedicel 4–9 mm long, glabrous; columella c. 1 mm long. *Seeds* 1.2–1.8 by 1–1.4 mm, minutely verrucate, rarely smooth, light brown, verrucae circular, randomly placed or longitudinally linear.
Distribution — Widespread, possibly introduced in multiple locations, occurring in most of southern Asia, ranging from Pakistan to Australia and the Pacific islands up to Hawai'i.
Habitat & Ecology — Ocurring in grassland, forests, swamps or cultivated fields, both in wet and dry soils. Often in disturbed, grazed or fire-damaged areas. Altitude: 0–1850 m. Flowering and fruiting all year round.
Uses — Used as an antiseptic, against intestinal parasites, eye diseases, cold, fever,

diarrhea, dysentery, itch, gonorrhea and (mammary) abscesses (A.C. Smith 1981; Quattrocchi 2016).

Vernacular name(s)— China: Huang zhu xi cao (Quattrocchi 2016). India: seed under leaf, virgate leaf-flower, banaunri, bhuiavali, bhiuavate, bhui-amla, biradi pello, bon baberi, jar amla, kaadu nelli, kadunelli,motibhuiavali, niruri, tanda meral, uchchi usirika, uchhiyusirka (www.flowersofindia.net; Quattrocchi 2016). Myanmar: shit-sha (W.J. Kress et al. 2003). Thailand: khaang amphai, luuk tai bai, phaeng kham hoi (Quattrocchi 2016). Laos: ket ‘hoy, ‘khi doy (Quattrocchi 2016). Vietnam: v[aar]y [oos]e (Quattrocchi 2016). Indonesia: sahakèpo, sakahepo (Indonesia, Heyne 1950, Quattrocchi 2016). Philippines: kaya-an, kayut-búlan, kayut-bulang (Merrill 1923, Quattrocchi 2016). Tahiti: tei ni niu (A.C. Smith 1981).

Notes — 1. According to Hunter & Bruhl (1997) the distinguishing character between *P. exilis* and *P. virgatus* is that the ovary of *P. exilis* is verrucate, and smooth in *P. virgatus*. However, smooth and verrucate ovaries occur in *P. virgatus* in areas outside Australia. See note under *P. exilis* for differences with *P. virgatus*. Additional distinguishing characters are the shape and size of the leaf blade, which is usually narrower and smaller in *P. exilis* and the diameter of the staminate flowers, which is also usually smaller in *P. exilis* than in *P. virgatus*.

2. *Phyllanthus narayanswamii* Gamble is here combined with *P. virgatus*. The differences described by previous authors to distinguish it from *P. virgatus* were a thickened revolute margin and subsessile staminate flowers. However, the margin differences are minimal and subsessile flowers can also be found in *P. virgatus*. The nervature of the leaves on the type of *P. narayanswamii* differs a little bit from other



Map 4-14 Distribution of *Phyllanthus virgatus* G. Forst.

specimens of *P. virgatus* in the prominent nervature on the lower side of the leaf blade.

23. Phyllanthus wheeleri G.L.Webster — Map 4-7

Phyllanthus wheeleri G.L.Webster (1995) 266; in Dassan. & Clayton (1997) 215; Chakrab. & N.P.Balakr. (2018) 309. — Type: *L.C. Wheeler 12437* (holo DAV; iso PDA, US), Sri Lanka, Central Province, Dambulla Rock.
Phyllanthus gardnerianus (Wight) Baill. var. *pubescens* Thwaites (1861) 282 (‘*gardneri*’). — *Phyllanthus simplex* Retz. var. *gardnerianus* f. *pubescens* (Thwaites) Müll.Arg. (1863) 33. — Lectotype: (designated by Webster 1995): *Thwaites C.P. 178* (K; iso PDA), Sri Lanka, Galagama.

Small shrubs , monoecious; branches brown, glabrous or hirsute, ridged, distally brown or sage-green, slightly flattened and with 2 larger ridges; internodes 2–5 mm long. *Stipules* triangular, 1–1.5 by 0.4–0.8 mm, base rounded, margin entire or erose, apex attenuate. *Leaves*: petiole c. 0.5 mm long, glabrous; blade elliptic or obovate, 5–13.5 by 2–7 mm, 1.8–2.4 times longer than wide, green, base asymmetric, obtuse, margin not thickened, slightly revolute, apex obtuse or rounded, younger leaves usually hirsute on both sides, older leaves often glabrous; midrib flat above, prominent underneath, lateral veins 5–7 per side, slightly prominent on both sides. *Staminate flowers* solitary or in pairs, c. 1 mm in diam; pedicel 2–2.5 mm long, glabrous, slender; sepals 6, elliptic, c. 1 by 0.5 mm, apex obtuse; disc glands 6, circular, c. 0.2 mm in diam, flat; stamens 3, c. 0.6 mm long, filaments free, reflexed, thecae ovoid, c. 0.2 mm long. *Pistillate flowers* solitary or in pairs, c. 1 mm in diam; pedicel 2.5–4 mm long, glabrous; sepals 6, ovate, c. 1 by 0.2 mm, apex acute; disc glands 6, sometimes sticking out between the sepals, cuneiform or obcordate, 0.2–0.5 by 0.2–0.3 mm, flat; ovary sessile, globular, c. 0.7 mm in diam, c. 0.7 mm high, densely hirsute; style absent, stigmas 3, c. 0.5 mm long, bifid for 3/4 of the length, reflexed. *Fruits* subglobular, 2–2.5 mm in diam, 6-grooved, hirsute, rarely glabrous; pedicel 3–4 mm long, glabrous; columella c. 1 mm long. *Seeds* c. 1–1.2 by 0.8–1 mm, smooth or verrucate, light brown, verrucae circular, in (indistinct) linear lines.
Distribution — Sri Lanka.
Habitat & Ecology — On shady and semi-shady red clay and sandy soils, often on road banks. Altitude: c. 230 m. Flowering and fruiting: October till May, possibly all year round.
Note — This species can be distinguished from other species of subgenus *Macraea* by the segmented pistillate flower disc. There are a few other species with a segmented pistillate disc: *Phyllanthus dumosus* has smaller orbicular leaves and the ovary is glabrous; *P. tenuipes* has the ovary on a gynophore and a style; *P. ussuriensis* has minute disc glands and glabrous, elliptic leaves; and *P. womersleyi* can be

distinguished by its (sub)orbicular leaves, prostrate habit and connate stamens.

24. Phyllanthus womersleyi Airy Shaw & G.L.Webster — Map 4-12

Phyllanthus womersleyi Airy Shaw & G.L.Webster in G.L.Webster & Airy Shaw (1971) 86; Airy Shaw (1980) 196; Punt (1980) 163. — Type: *NGF* (*J.S. Womersley) 11311* (holo K; iso A, BISH, BRI, CANB, L (L0016456), Papua New Guinea, Western Highlands, Wabag Sub-district, Merimanta, Porget logging area.

Prostrate herbs or subshrubs, sometimes erect, then up to 150 cm high, monoecious; branches brown, red or purple, glabrous, with 2 minute ridges, often partly without leaves, but with persistent stipules; internodes 0.5–4 mm long; aerial roots occasionally present on nodes when prostrate, up to 0.5 mm thick. *Stipules* irregularly orbicular, 1–1.8 mm in diam, base rounded, margin erose, sometimes entire or spinose, apex rounded. *Leaves*: petiole c. 0.5 mm long, glabrous; blade (sub)orbicular, rarely ovate, 2–4 mm in diam, about equally long as wide, glabrous, grey-green when dry, sometimes with red hue, base rounded or obtuse, margin not thickened, flat, apex rounded, rarely obtuse; midrib sunken above, prominent underneath, lateral veins 4 or 5, barely visible. *Staminate flowers* solitary, 2.5–3 mm in diam; pedicel c. 3 mm long, glabrous; sepals 6, elliptic, apex rounded, red, in two whorls, outer ones c. 1.2 by 0.8 mm, inner ones c. 1 by 0.6 mm; disc glands 6, oblate, c. 0.5 mm in diam, c. 0.1 mm high, foveolate; stamens 3, c. 0.9 mm long, filaments connate at base, reflexed, robust, thecae subglobular, c. 0.2 mm long, bright yellow; for pollen see Punt (1980) and Wu et al. (2016). *Pistillate flowers* solitary, 2.5–3 mm in diam; pedicel 3–4 mm long, glabrous; sepals 6, elliptic, c. 1.2 by 0.8 mm, red, apex rounded or obtuse; disc glands 6, oblate, c. 0.5 mm in diam, c. 0.1 mm high, foveolate, flat, in fruit merging and flattened, then minutely foveolate; ovary sessile, ovoid, c. 0.5 by 0.5 mm, verrucose; style absent, stigmas 3, c. 1 mm long, thin, bifid for half of the length, reflexed. *Fruits* subglobular, 2–2.5 mm in diam, 6-grooved, red or purple, basally glabrous, apically verrucose or lepidote; pedicel 3–5 mm long, glabrous; columella c. 1 mm long. *Seeds* c. 1.5 by 0.6 mm, smooth, chestnut-brown.
Distribution — Papua New Guinea (Southern and Western Highlands).
Habitat & Ecology — In forests, grassland, on exposed or open patches, amongst pit-pit (*Saccharum edule* Hassk., Poaceae), or in ground cover beneath *Rhodondendron* and fern species. Common on drier ground, but also found on a saturated swampy lake-margin. Altitude: 2250–3270 m. Flowering and fruiting: April to December.
Uses — Eaten by pregnant women, who hope to have a son, especially if they only had daughters so far (*Bowers 59*).
Vernacular names —Nom, Noma (Tomba), Nohm (Enga, Poio dialect), Num (Enga, Kepilaum dialect), Nomə k'omə (Medlpa, Kaugel dialect; partly after Webster & Airy Shaw (1971).

Note — *Phyllanthus womersleyi* is the only species in *Macraea* with fully connate filaments, which, together with its small orbicular leaves and general prostrate habit, makes it easily distinguishable from related species. The filaments in *P. ridsdalei* are often variably connate and may appear similar, but the pistillate flowers (with excerted style) in that species are quite distinctive. They also do not overlap in distribution.

Acknowledgements
Dr. P.H. Hovenkamp is thanked for discussing the validity of Brunel (1987), why it should be acknowledged according to the Melbourne Code and for finding the proper author of *Phyllanthus myrtifolius.* The Queensland Herbarium (BRI), Australian National Herbarium (CANB), University of California Davis Center for Plant Diversity (DAV), Conservatoire et Jardin botaniques de la Ville de Genève (G), Harvard University Herbaria (A), Royal Botanic Gardens Kew (K), Naturalis Biodiversity Center (L), Missouri Botanical Garden (MO), Royal Botanic Gardens, National Herbarium of New South Wales (NSW), Muséum National d'Histoire Naturelle (P), Swedish Museum of Natural History (S) and United States National Herbarium, Smithsonian Institution (US) are gratefully acknowledged for lending us the material used for this revision. Two anonymous reviewers are thanked for their comments on the manuscript, which greatly improved the manuscript. The last author thanks the Treub Maatschappij, the Society for the Advancement of Research in the Tropics, for supporting the Ornstein university chair in Tropical Plant Biogeography.

Identification list of Phyllanthus specimens

1 = *Phyllanthus aoraiensis* Nadeaud
2a = *Phyllanthus chrysanthus* Baill. var. *chrysanthus*
2b = *Phyllanthus chrysanthus* Baill. var. deverdensis M.Schmid
2c = *Phyllanthus chrysanthus* Baill. var. micrantheoides (Baill.) M.Schmid
3 = *Phyllanthus clarkei* Hook.f.
4 = *Phyllanthus distichu*s Hook. & Arn.
5 = *Phyllanthus dumosus* C.B.Rob.
6 = *Phyllanthus everettii* C.B.Rob.
7 = *Phyllanthus exilis* S.Moore
8 = *Phyllanthus gardnerianus* (Wight) Baill.
9a = *Phyllanthus glaucophyllus* Sond. var. *glaucophyllus*
9b = *Phyllanthus glaucophyllus* Sond.var. *alpestris* (Beille) Verwijs
10 = *Phyllanthus lancifolius* Merr.
11 = *Phyllanthus macraei* Müll.Arg.
12 = *Phyllanthus minutiflorus* F.Muell. ex Müll.Arg.
13 = *Phyllanthus myrtifolius* (Moon ex Wight) Müll.Arg.

14 = *Phyllanthus pacificus* Müll.Arg.
15 = *Phyllanthus prominulatus* J.T.Hunter & J.J.Bruhl
16 = *Phyllanthus ridsdalei* R.W.Bouman & Verwijs
17 = *Phyllanthus samarensis* Müll.Arg.
18 = *Phyllanthus tararae* Verwijs
19 = *Phyllanthus tenuipes* C.B.Rob.
20 = *Phyllanthus urceolatus* Baill.
21 = *Phyllanthus ussuriensi*s Rupr. & Maxim.
22 = *Phyllanthus virgatus* G.Forst.
23 = *Phyllanthus wheeleri* G.L.Webster
24 = *Phyllanthus womersleyi* Airy Shaw & G.L.Webster

JG Adam 44: 9b; 3647: 9b; 4186: 9b; 4868: 9b; 5181: 9b; 6258: 9b; 12802: 9b; 20644: 9b; 20670: 9b; 21585: 9b; 24043: 9b; 27416: 9b; 28786: 9b; 29794: 9b — L Anglade 164: 11; 537: 22; 886: 11 — ANU series 597: 24; 911: 24 — CM Arora 5616: 22 — Asdat 197: 22 — Aubreville-Heine 248: 2a — LV Averyanov HLF 4144: 22.

RC Bakhuizen van den Brink Jr 1873: 22; 3484: 22 — B Balansa 1214: 1c; 1216: 2a; 1860: 2a; 1861: 2a; 1862: 1c; 2790: 1c — J Banks & Solander 1769: 20 — ME Barker 39: 9 — A Baudouin 542: 1c — MG Baumann-Bodenheim 5575: 1c; 14333: 22 — MG Baumann-Bodenheim & A. Guillaumin 9453: 1c; 9613: 1c; 9619: 1c — AR Bean 16608: 12; 24126: 7 — H Beckler 668: 22 — E Bidault et al. 260: 9b; 334: 9b — D Bilivogui et al. 62: 9b — ST Blake 17662: 7; 23241: 12 — JP Blanchon 1335: 2a — E Blatter & Hallberg 24797: 8 — R Booth 4185: 7 — R Booth & D Kelman 3263: 12; CAM 14-9: 12 — R Booth & EJ Thompson 3942: 12 — AS Boughey GC 18095: 9b — Bourdillon 7: 8 — AG Bourne 448: 8; 1404: 11; 2861: 8 — N Bowers 59: 24 — LJ Brass 6516: 22; 7525: 22; 8451: 22; 8651: 18; 21666: 22; 22101: 22; 27727: 22; 6516A: 18 — BS series 13306: 26; 15879: 19; 17465: 17; 24460: 17; 29469: 22; 35655: 17; 43249: 17; 43284: 17; 75281: 17; 85215: 22 — W Bush 8013: 2.

BJ Carter 404: 7; 651: 12 — H Cheng 163404: 22 — AJB Chevalier 12907: 9b — China Germany Team 136: 22 — GM Chippendale 1063: 7; 5742: 12; 5955: 7; 6113: 7; 7554: 7 — E Christophersen 1272: 2 — E Christophersen et al. 1523: 2 — CB Clarke 25420: 3 — JR Clarkson 3565: 12; 7304: 12 — JR Clarkson & VJ Neldner 9001: 12; 9465: 22 — MS Clemens 43372: 22 — NHA Cole 200: 9b — DJ Collins 1845: 22 — RG Cooray 69111805R: 22 — ID Cowie 2586: 12; 4386: 12; 11937: 7 — ID Cowie & J Palmer 13414: 7 — LH Cramer 3382: 13 — LA Craven 3315: 12 — NEG Cruttwell 8: 22 — RJ Cumming 17583: 12; 21276: 12; 24807: 12.

JJFE de Wilde 888: 9b — WJJO de Wilde & BEE de Wilde-Duyfjes 6873: 9b; 18943: 22 — BG Decker 2011: 22; 2299: 22; 2639: 22 — O Degener 4145: 4; 8019: 4; 8029: 2 — O Degener & I Degener 28389: 4; 28734: 2 — O Degener & T Murashige19952: 2 — O Degener & K Nitta 8018: 2 — O Degener & E Ordonez 12185: 4; 14 — O Degener & CL Shear 8026: 2 — O Degener et al. 8014: 4; 8017: 4; 11645: 4; 11645: 4; 12360: 4; 12509: 4; 12682: 4; 20797: 4; 24152: 4; 25115: 4; 25115: 4 — FC Deighton:

5637 5b; 5638: 9b — SW Deng 90793: 22 — E Deplanche 503: 2b — A Dietrich 2666: 22 — WA Docters van Leeuwen 1860: 22 — JR Drummond 26379: 22 — CR Dunlop 2405: 22 — L Dunn 247:21 — L Dunn & DH Lorence 479: 22.
ADE Elmer 11023: 22; 12018: 22; 17442: 22 — HJ Esser 98-187: 22; HD Everett 4301: 6.
F Fagerlind 673: 13; 6122: 8; 6632: 22; 6663: 4 — F Fagerlind & C Skottsberg 6420: 4 — CS Fan & YY Li 489: 22 — U Faurie 484: 4; 489: 4; 3822: 21; 6121: 21 — KM Feng 12528: 22 — J Florence 2400: 13; 4201b: 22; 4297: 22; 4776: 20; 4813: 20; 4923: 20; 6718: 22; 6836: 22; 7812: 20;8321: 20; 8386:21; 8429: 22; 8503: 22; 9305: 20; 11881: 20 — J Florence & S Perlman 9574: 22; 9639: 22 — T Flynn & D Harder 3005: 4 — CN Forbes 42.Mo: 4; 45.2: 4; 431.Mo: 4; 720.R: 4; 1046.O: 4; 1520.O: 4; 1669: 4; 1669.O: 4 — PI Forster & R Booth 22524: 12 — PI Forster & MB Thomas 37074: 12 — FR Fosberg 10731: 4; 12296: 4; 12410:4; 13399: 4; 37939: 22; 38168: 22; 50670: 13; 61028: 13; 62875: 13 — FR Fosberg & M-H Sachet 53167: 23 — FR Fosberg & H St John 8909: 4 — I Franc 295: 22;788: 2a; 1385: 1c; 2049: 22 — H Fung 20309: 22 — M Furuse 44623: 21.
BH Gagné 1223: 22 — JS: Gamble 3010: 8; 11445: 8; 12015: 8; 18744: 13; 20611: 8 — G Gardner 772: 8 — G Gaudichaud-Beaupré 289:4; 290: 4 — C Geerling & J Bokdam 1685: 9b — JW Gillespie 4759: 22 — GW Gillet 2199: 22 — ML Grant 5378: 20 — AJC Grierson & DG Long 2415: 22 — A Guillaumin & MG Baumann-Bodenheim 9208: 22; 9543: 1c; 11190: 1c; 12214: 1c; 12235: 1c; 1c; 13483: 22.
JH Haas 2834: 3; 2855: 3 — PK Haba et al. 75: 9b; 123: 9b; 160: 9b — F Hallé 2060: 22; 2061: 22; 2086: 22 — H Hara et al. 6306814: 22 — AA Heller 2196: 4 — D Herbst 2360: 4 — D Herbst & J Obata 5262: 4 — W Hillebrand 52: 4; 53: 4; 54: 4; 2340a: 4 — RF Hohenacker 1130: 8 — RD Hoogland & R Pullen 6006: 24 — RD Hoogland & R Schodde 7078: 24; 7567: 24 — Hort. Bog. Coll. 147:20; 149: 17 — SY Hu & KH Yung 413: 13 — CE Hubbard & CW Winders 7671: 12 — JT Hunter, JJ Bruhl & JL Egan 152: 7; 1549: 7; 1576: 12; 1590: 12 — PCM Hutchinson & J Obata 2809: 4 — SY Hutchinson & J Obata 12264: 22 — BPM Hyland 7190: 22.
MM Jacobs 7713: 19 — P Jaeger 1373: 9b — T Jaffré 1240: 2a; 1576: 2a — RL Jago 6426: 12 — PCM Jansen & C Boane 7889: 9a — DES Jardin 122: 22 — AHM Jayasuriya 949: 8; 1359: 13 — AHM Jayasuriya & S Balasubramanium 1210: 8 — AHM Jayasuriya et al. 1472: 8 — DMA Jayaweera 357: 13 — R Jensen & J Kemp 2610: 12 — J Jeswiet 753: 22 — RW Johnson & MB Thomas MRS 546: 7; MRS 958: 12 — CCH Jongkind & D Bilivogui 11355: 9b — CCH Jongkind et al. 7423: 9b; 7758: 9b; 11018: 9b; 11113: 9b.
A Kanis 1835: 12 — HS Kathriarachchi et al. 4: 8; 23: 13; 42: 8 — DT Kelman 1001: 12 — J Kemp 8089: 12 — KF Kenneally 11474: 12 — GK Kjellberg 165: 22 — J Klackenberg & R Lundin 97: 8 — A Kleinhoonte 747: 13 — AJGH Kostermans 716: 17; 7872: 17; 24298: 13; 25142: 13 — KU Kramer & GB Nair 6130: 8.
LAE series 60791: 24; 66177: 24 — CE Lane-Poole 424: 9b — KM Larsen et al. 31536: 22 — PK Latz 6121: 12 — SK Lau 3345: 22; 4216: 22; 6397: 22 — MO

Lazarides 7739: 22; 9248: 12 — GJ Leach 4100: 7 — J Lépine 138: 20 — YH Li 738: 22 — BH Liang 83336: 22 — XR Liang 65717: 22 — JC Liao 10549: 13 — E Licent 7837: 22 — Lingnan (To and Ts'ang) 12744: 22 — S Lisowski 12682: 9b; 51627: 9b; D-718: 9b.

HS MacKee 2479: 1c; 3683: 1c; 4241: 1c; 4570: 2a; 12511: 2a; 13306: 2a; 13565: 2a; 14555: 2a;15238: 2a; 15240: 2a; 15289: 2a; 15294: 2a; 16614: 2a; 16832: 2c; 16901: 2a; 16917: 1c; 19414: 2a; 20340: 1c; 21229: 2a; 21926: 2a; 22608: 1c; 23177: 2a; 23340: 2a; 23906: 2c; 25137: 2a; 27419: 2a; 28399: 2a; 30021: 2b; 30410: 2a; 30781: 2c; 30782: 2c; 31158: 2a; 35415: 2a; 36769: 2c; 36868: 2a; 36868: 2a; 37091: 2a; 37943: 2c; 40357: 2c; 40548: 2a; 42559: 2a — T Makino 33797: 21 — R Malaise 432: 22 — C Mas et al. 1315: 9b — JF Maxwell 03-251: 22; 04-371: 22; 04-371: 22; 06-389: 22; 06-415: 22; 85-814: 22; 86-849: 22; 90-616: 22; 90-957: 22; 91-1063: 22; 92-435: 22; 94-704: 22; 98-585: 13; 99-166: 22 — KR McDonald 5983: 12; 6686: 12; 7530: 12; 8109: 12; 8350: 12; 8399: 12; 9514: 12 — GD McPherson 5340: 2c; 5543: 2c; 6210: 2b — GD McPherson & HH van der Werff 17703: 2c; 17704: 2c; 17878: 2a — W Meijer Ceylon 1457: 13 — R Melville 3732: 22 — Mereir 272: 22 — ED Merrill 164: 6; 292: 22; 2885: 6; 3343: 22; 4299: 19; 6680: 19 — ED Merritt & Darling 13974: 5 —TL Mitchel 66: 22 — S Mokim 89: 22 — HF Mooney 3971: 22 — JW Moore 100: 22 — JK Morton & D Gledhill SL 1056: 9b; SL 3132: 9b — A Mouly 516: 22 —EP Mumford 488: 22 — J Munzinger 380: 2a — J Munzinger & GD McPherson 796: 2a — L Murray et al. 49: 22.

J Nadeaud 458: 20; 459: 1 — V Narayanswami 640: 22 — VJ Neldner 4498: 12 — NGF series 11311: 24; 16667: 22; 41245: 24; 45070: 22 — DH Nicolson et al. HFP 2817: 22 — A Nothis 478: 2a.

E Ordonez 12847: 4.

J Palmer & ID Cowie 894: 12 — JF Pancher 165: 2b; 362: 20; 365: 2c; 5855: 20 — Park 57: 21 — MO Parker 739: 12 — RN Parker 2389: 22 — HE Parks 16244: 22 — M Parris 9375: 12 — S Perlman 10112: 22; 14972: 22; 15013: 22; 18443: 22 — S Perlman et al. 10158: 22 — S Perlman & KR Wood 15969: 22; 15985: 22; 19193 — S Perlman et al. 14922: 22 — A Pételot 6563: 22 — PNH series 4425: 19; 12547: 22; 15482: 17; 17040: 22; 18667: 22; 35919: 22; 35955: 22; 39087: 22; 117300: 17; 117902: 17 — E Poilane 17382: 22 — P Poilecot 0966 CI: 9b — R Pooma et al. 2760: 21 — PPI series 3439: 17; 5748: 17; 5766: 17; 5969: 17; 6034: 17; 7383: 17; 7550: 17; 7746: 17; 10066: 17; 10071: 17; 10505: 17; 15475: 13; 20201: 17; 20230: 17; 21911: 17 — RL Pullen 9118: 12 — W Punt 797: 11.

EH Quayle #X: 22; 1341: 22; 1781: 22.

TP Ramamoorthy HFP 1832: 22 — M Ramos 1489: 22; 1950: 22 — MO Rankin 1164: 12; 2074: 12; 2162: 12 — FW Rappard 141: 22 — EJ Rémy 601: 4; 603: 4 — Rheede 10: 22 — CE Ridsdale 1479: 24 — CE Risdale et al. ISU 276: 19 — RHT series 16359: 21; 18224: 22 — Ribourt 72: 20 — CB Robinson 1704: 17 — G Roberty 5188: 22 — JF Rock 4811: 4.

Sanderson 447: 9 — MJS Sands et al. 6551: 22 — A Saulière 96: 11; 101: 11 — JC

Saunders 651: 24 — PA Schäfer 5813: 22; 5915: 22; 5955: 22 — FRR Schlechter 14803: 22;14832: 2a; 14832: 22; 15020: 2a & 14 — M Schmid 1466: 2a; 5370: 2a; 5363 bis: 2a — E Schmutz 5745: 17; 7138 — R Schnell 7141: 9b; 7255: 9b — M Schultz 660: 22; 668: 22 — GF Scott-Elliot 3962: 9b; 5819: 9b — OH Selling 257: 2a — WA Setchell & HE Parks 1: 22 — SFN series 35488: 13 — Shan Ranrong et al. 7400: 21 — T Shimizu et al. T-10701: 22; T-10110: 3 — MA Siddiqi 27700: 22 — MP Simmons 1827: 2a — ELAN Simons et al. 833: 9b — C Skottsberg 302: 4 — LS Smith 3060: 22 — DD Soejarto et al. 8163: 22 — SH Sohmer & D. Herbst 6137: 4 — T Sørensen et al. 7315: 22 — RL Specht 222: 7; 322: 7; 517: 12; 747: 12; 958: 12 — H St John 17985: 4; 24910: 4; 25169: 4 — H St John & AJ Eames 18737: 4 — H St John & RS Cowan 22599: 4 — AN Steward et al. 635: 22 — BC Stone 3164: 4 — B Suprin 1925: 2a; 1989: 2a; 2177: 2c.

T Takahashi 341: 21 — PM Taylor 2585C: 17 — SW Teng 90793: 22 — NW Thomas 580: 9b — EJ Thompson & M Newton BUR 272: 12; WES 1071: 12 — EJ Thompson & GP Turpin NOR 246: 12; NOR 258: 12 — EJ Thompson & GW Wilson WES 1376: 12 — BG Thomson 2209: 7 — EJ Thomson WES 252: 7; WES 271: 7; WES 526: 7; WES 1007: 7; WES 1102: 7; WES 1142: 7 — RF Thorne 28254: 2c — GHK Thwaites CP 5: 22; CP 178: 23; CP 501: 8; CP 650: 13 — C Tirel 1260: 2a — M Tobe 15505: 21 — C Townsend & TP Ramamoorthy 60: 8 — FRR Tronchet 654: 2c — S Tsugaru 20997: 21 — S Tsugaru & T Takahashi:29875: 21 — S Tsugaru et al. 34844: 21.

MMJ van Balgooy 2953: 22; 5069: 17 — XM van der Burgt & C Couch 1156: 9b — HH van der Werff 11775: 22; 11776: 22 — CGGJ van Steenis 19516: 13 — JAJ Verheijen 1366: 17; 1367: 17; 1368: 17 — JM Veillon 1406: 2a; 1485: 2a — E Vieillard 336: 20; 1196: 2c; 1197: 22; 1199: 22; 1201: 2a; 2073: 2c; 3197: 2a; 3200: 2b; 3201: 2b; 3202: 22 — K Vollesen MCR 4467: 9a — KM Vongkuna 14: 22.

WL Wagner & D Lorence 6227: 22 — PP Wan & KS Chow 79149: 22 — C Wang 33013: 22 — CW Wang 79987: 22 — ZT Wang et al. 395: 21 — BS Wannan 1191: 12 — BS Wannan & P Graham 2799: 7 — H Wanntorp & HE Wanntorp 2527: 8 — BM Waterhouse & AD Rice 8064: 12 — JZ Weber 1046: 22 — GL Webster 19325: 2c — GL Webster & T Jaffré 19253: 2c — K Weinland 241: 22; 389a: 22 — LC Wheeler 12437: 23; 12955: 23; 12961: 23; 12965: 23 — LC Wheeler & N Balakrishnan 12551: 23; 12590: 23 — R Wight KD 2581: 11; KD 2584: 8 & 14; KD 2656: 22 — GM Wightman 20: 15 — RL Wilbur 406: 4 — C Wilford 66: 21 — GH Wilkins 109: 7 — JS Womersley 11311: 24 — KR Wood 10251: 22; 10289: 22 —KR Wood & JY Meyer 10516:21 — KR Wood & S Perlman 6540: 22 — KR Wood et al. 6506: 22 — KR Wood et al. 1760: 4.

K Yonekura 10571: 21 — GC Yong 200643669: 21 — TT Yü 17449: 22 — ML Yu & PT Li 37: 21; 86: 21 — TG Yuncker 15125: 22; 15339: 22.

PCM Zeng 10302: 22 — CLP Zeyer 1509: 9a — ZQ Zhang 136: 22 — H Zollinger 46: 22.

CHAPTER 5

LECTOTYPIFICATION AND AMENDED DESCRIPTION OF PHYLLANTHUS (PHYLLANTHACEAE) SPECIES DESCRIBED BY KOORDERS FROM SULAWESI, INDONESIA

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Peter C. van Welzen

Published in Reinwardtia 18 (2): 97-103. 2019

https://doi.org/10.14203/reinwardtia.v18i2.3781

Chapter 5

LECTOTYPIFICATION AND AMENDED DESCRIPTION OF PHYLLANTHUS (PHYLLANTHACEAE) SPECIES DESCRIBED BY KOORDERS FROM SULAWESI, INDONESIA

Short title: On *Phyllanthus* (Phyllanthaceae) from Sulawesi

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ABSTRACT

Two species of *Phyllanthus* collected and described by Koorders during his travels on the island of Sulawesi (Indonesia) are lectotypified, descriptions amended and their taxonomic affinity is discussed. *Phyllanthus mindorensis* was found to be too similar to *P. celebicus* and is placed in the synonymy of the latter. A key is provided to the species of *Phyllanthus* on Sulawesi.

Keywords: Celebes, *Eriococcus*, Koorders, Euphorbiaceae s.l., Phyllantheae, *Phyllanthus*, Sulawesi, Taxonomy

Introduction

The flora of Sulawesi represents an interesting biodiversity hotspot that borders several biogeographical zones, with the Sunda shelf to the west, the Sahul shelf to the east and the Philippines to the north (Stelbrink et al. 2012). It is the largest island of Wallacea, a biogeographic region that also includes the Moluccas, the Lesser Sunda Islands (Dickerson 1928), and botanically usually also the Philippines (van Welzen et al. 2011). While this island has become better explored recently, the flora remains understudied and many taxa did not receive any taxonomic treatment for some time. The enumeration of Euphorbiaceae for Central Malesia by Airy Shaw (1982) lists ten species of *Phyllanthus* L. for Sulawesi (table 1), but this was only based on a limited number of collections. Airy Shaw (1982) made no redescription of the species and did not treat the Wallacean islands extensively like he did for Borneo (Airy Shaw 1975) and Papua New Guinea (Airy Shaw 1980). Several species are probably still undiscovered and it is important that an adequate comparison can be made between those previously described from the island. Koorders (1898) reported two new species of *Phylllanthus* (*P. celebicus* Koord. and *P. minahassae* Koord.) in his travel account of the island, but only included a brief description of their habit with no mention of flower morphology. During the preparations for

Table 5-1. Species of *Phyllanthus* in Sulawesi, compiled from Robinson (1909), Airy Shaw (1982) and supplemented by records from the L herbarium. Species are listed by subgenus following Bouman et al. (2018). *Phyllanthus mindorensis* was listed by Airy Shaw (1982) and is treated here as synonym.

Subgenus	**Species**
Eriococcus (Hassk.) Croizat & Metcalf	*Phyllanthus buxifolius* (Blume) Müll.Arg.
	Phyllanthus celebicus Koord.
	Phyllanthus lamprophyllus Müll.Arg.
	Phyllanthus minahassae Koord.
	Phyllanthus trichosporus Adelb.
Macraea (Wight) Jean F.Brunel	*Phyllanthus lancifolius* Merr.
	Phyllanthus samarensis Müll.Arg.
	Phyllanthus virgatus G.Forst.
Gomphidium (Baill.) G.L.Webster	*Phyllanthus tenuirhachis* J.J.Sm.
Kirganelia (A.Juss.) Kurz	*Phyllanthus reticulatus* Poir.
Emblica (Gaertn.) Kurz	*Phyllanthus urinaria* L.
Swartziani (G.L.Webster) Ralim. & Petra Hoffm.	*Phyllanthus amarus* Schumach. & Thonn.
Afroswartziani Ralim. & Petra Hoffm.	*Phyllanthus debilis* Klein ex. Willd.

a new classification of the genus *Phyllanthus* several taxonomic problems were identified, often concerning rare species (Bouman et al. 2018). This included the species of Koorders (1898), which could not yet be placed in any subgeneric group of *Phyllanthus* (Bouman et al. 2018).

During a recent visit to the Herbarium Bogoriense (BO) on Java by the first author, the types of the Koorders' species could be studied. Here, we place these species in *Phyllanthus* subgenus *Eriococcus* (Hassk.) Croizat & Metcalf section *Eriococcus* and expand the descriptions of both species. Affinities to, and differences with, other species are discussed and a provisional key to the known *Phyllanthus* species of Sulawesi is provided.

Taxonomic treatment

Both species discussed here are placed in *Phyllanthus* subgenus *Eriococcus* section *Eriococcus* based on the morphology of the staminate flowers. The staminate flowers in both species consist of four sepals in a cross shape with fimbriate margins, four disc glands and two connate stamens with horizontally dehiscing anthers. This is consistent with *Phyllanthus* subgenus *Eriococcus* section *Eriococcus* (see Müller 1866) and both species are classified here in this taxon. Subgenus *Eriococcus* section

Emblicastrum Müll.Arg., which is represented by *P. lamprophyllus* Müll.Arg. on Sulawesi, differs in the usually upright orientated sepals with entire margins, thicker leaves and the presence of a tubular style. No species of section *Eriococcus* is endemic to Papua New Guinea (Bouman et al. 2018) and the closest affinity of both species are similar *Phyllanthus* species of the Philippines. Roughly ten species of section *Eriococcus* occur on the Philippines and they are very similar in staminate flower and leaf morphology. Unfortunately many of these have been rarely collected. Differences for identification with the Philippine species are discussed below in the notes under the species, but they undoubtedly represent the closest relation to the species of Sulawesi within subgenus *Eriocccus*. A provisional key for *Phyllanthus* in Sulawesi is provided. Information for the key was derived from herbarium specimens, Luo et al. (2011a), Robinson (1909) and Verwijs et al. (2019). All acronyms for herbaria follow Thiers (2019, continuously updated).

Key to the *Phyllanthus* species of Sulawesi

1. Branching non-phyllanthoid (laminate leaves on main axes present, lateral branches subtended by leaves and not deciduous); stamens 3, filaments free; fruits capsules — subgenus *Macraea* 2
1. Branching phyllanthoid (leaves on main axes reduced to cataphylls, lateral branchlets bear laminate leaves and are deciduous); stamens 2, 3 or 5; filaments free or connate (or in whorls); fruits capsules or berries.................4

2. Prostrate or erect herbs or subshrubs, up to 1 m high, axes glabrous; pistillate pedicel 3–9 mm long ....*P. virgatus*
2. Erect shrubs to trees, up to 2 m high, axes mostly pubescent; pistillate pedicel 8–50 mm long...3

3. Leaf blades mostly ovate-elliptic, 9‒79 mm long, apex acuminate; staminate sepals 1.1–1.4 × 0.5-0.8 mm; pistillate pedicel 8–50 mm long...... *P. lancifolius*
3. Leaf blades elliptic, 7‒24 mm long, apex acute to obtuse or rounded to retuse; staminate sepals 1.2–1.6 × 0.6–0.8 mm; pistillate pedicel 8–10 mm long......*P. samarensis*

4. Herbs (or only woody at the base)..5
4. Shrubs to trees 7

5. Pistillate inflorescences at basal part of lateral branchlets; ovary warted; seeds with transverse ridges— subgenus *Emblica*...................................... *P. urinaria*
5. Pistillate inflorescences at distal part of lateral branchlets; ovary smooth; seeds smooth or with longitudinal striae..6

6. Leaf blades oblong, apex rounded, upper side green; inflorescences mostly

bisexual; staminate flowers with 5 sepals— subgenus *Swartziani* .....*P. amarus*

6. Leaf blades ovate, apex acute, upper side dark green; inflorescences unisexual; staminate flowers with 6 sepals— subgenus *Afroswartziani* ....*P. debilis*

7. Staminate flowers with 5 sepals, stamens 5, fused in 2 whorls; stigmas entire; fruits berries— subgenus *Kirganelia*..*P. reticulatus*

7. Staminate flowers with 4 or 6 sepals, stamens 2 or 3, filaments free or connate in one whorl; stigmas bifid or entire (not seen in *P. minahassae*); fruits capsules...8

8. Leaves usually symmetric, blade elongated eliptic-ovate, longer than 5 cm; sepals 6 in both flowers of both sexes; stamens 3, filaments free, anthers dehiscing vertically — subgenus *Gomphidium* ....*P. tenuirhachis*

8. Leaves usually basally asymmetric, blade elliptic or ovate; shorter than 4.5 cm; sepals in staminate flowers 4, pistillate flowers with 5 or 6 sepals; stamens 2, filaments connate, anthers dehiscing horizontally— subgenus *Eriococcus*.9

9. Leaves coriaceous; staminate sepals erect, tubular, margins entire............... 10

9. Leaves membranous to slightly coriaceous; staminate sepals spreading, margins fimbriate, dentate or laciniate.. 11

10. Leaf blades up to 4 cm long; filaments of stamens thickened at apex; ovary 4–8-locular; style absent, stigma almost entire with only a bilobed fold at apex...*P. buxifolius*

10. Leaf blades up to 1.2 cm long; filaments of stamens slender; ovary 3-locular; style present, tube of c. 2.2 mm, stigmas entire.........................*P. lamprophyllus*

11. Branchlets 8–10 cm long, glabrous; capsules glabrous, smooth; seeds c. 1.8 mm high..*P. trichosporus*

11. Branchlets 17–40 cm long, pubescent; capsules verrucate or smooth and puberulous; seeds c. 2–4.8 mm high.. 12

12. Leaf blades shorter than 22 mm; sepals red to brown; pistillate sepals not enlarged in fruit, shorter than 4 mm; fruit pedicel up to 3.5 cm long........1. *P. celebicus*

12. Leaf blades longer than 25 mm; sepals pale green; pistillate sepals enlarged in fruit, up to 16 mm long; fruit pedicel 3–4 cm long...................2. *P. minahassae*

Note

Phyllanthus subgenus *Kirganelia* is represented by *P. reticulatus* Poir. on Sulawesi, though there is some discussion on how to differentiate it from *P. microcarpus* (Benth.) Müll.Arg. In the flora of Thailand (Chantaranothai 2007), they are distinguished based on the presence or absence of indumentum while Luo et al.

(2011a) distinguish them based on habit and floral characters. Specimens from Sulawesi seen for this study were characterized by emergent styles and sometimes bisexual inflorescences while there were both pubescent and glabrous forms present. This conforms to the definition Luo et al. (2011a) for *P. reticulatus* and it is treated as such here.

Species descriptions of *P. celebicus* and *P. minahassae*

1. Phyllanthus celebicus Koord.,
Phyllanthus celebicus Koord., Meded. Lands Plantentuin 19: 588, 627 (Koorders 1898). —
Lectotype (designated here): Indonesia, Sulawesi, Minahasa province (Menado), near Pinomorongan, near Kajoewatoe, *H.S. Koorders 16949* (fieldnumber 1917) (lecto BO (BO129623); isolecto L (L.2246433, L.2246434).
Phyllanthus mindorensis C.B.Rob., Philipp. J. Sci., C 4: 82 (Robinson 1909). — Type: *L.M. Merritt 5370* (not traced); paratype: Philippines, Mindoro, *L.M. Merritt 8789* (K (K001056684)); paratype *L.M. Merritt 8606* (not traced). **Syn. nov.**

Shrubs, 0.5–1 m high, monoecious, all axes puberulent to pubescent with dark brown short stiff hairs; branching phyllanthoid; branchlets terete, 17–26 cm long, bearing 32–56 leaves, internodes 2–3 mm long. *Cataphyllary stipules* triangular, c. 1.5 × 2 mm, membranous, caducous, base plane, tending to fuse with cataphyll, margin entire, apex acute. *Cataphylls* triangular, 1–1.5 × c. 1 mm, membranous, caducous, margin entire, apex acute. *Stipules* triangular, c. 1 × 0.5 mm, caducous, membranous, base plane, margin brittle, apex acute. *Leaves* distichous; sessile to petiole 0.5–1 mm long, glabrous; blade elliptic, asymmetric, 10–21 × 5–7.5 mm, 2–3.2 times longer than wide, membranous to slightly coriaceous, base cuneate, margin slightly thickened and slightly revolute, apex rounded, mucronate, mucro 0.1–0.2 mm long, glabrous except for some hairs on basal part of lower side, upper side darker green; venation pinnate, midrib prominent, flat on both sides, lateral veins 4–6 per side, indistinct. *Inflorescences* axillary fascicles, usually unisexual and originating from small brachyblasts, up to 4 staminate flowers together near basal part of branchlets, pistillate flowers solitary on distal part of branchlets. *Staminate flowers* c. 1.1 mm in diameter closed, 2.2–3.5 mm when open; pedicel 4.5–5 mm long, terete, glabrous, thin; sepals 4, ovate, 1–1.5 × 0.8–1.1 mm, spreading, red-brown, margin dentate to laciniate, apex acute, midrib indistinct; disc glands 4, alternating with sepals, obovate, 0.2–0.3 × 0.3–0.6 mm, indented from thecae; stamens 2, 0.4–0.5 mm long, filaments and connectives connate, filaments c. 0.2 mm high, anthers slightly stipitate resulting in cross-shaped connective, apically extended for c. 0.1 mm, thecae oblong, c. 0.3 × 0.2 mm, hanging above disc gland, dehiscing horizontally via slits. *Pistillate flowers*: pedicel c. 16 mm long, terete, pubescent, thin; sepals 5, ovate, c. 1.5 x 1.1 mm, red-brown, margin fimbriate to laciniate, apex acute, midrib indistinct; disc annular, strongly star-shaped, c. 0.8 mm in diameter at shortest point, with large oblong lobes alternating with sepals, lobes 0.3–0.7 mm long and c. 0.2 mm wide, slightly thickened at the end; ovary globose, c. 1.3 mm wide, c. 1.1 mm high, puberulous; style absent; stigmas 3, bifid for entire length, c. 0.2 mm long, curved upwards. *Fruits* capsules, only dehisced remains left; pedicel terete, 1.8–3.5 cm long, greenish, puberulous, rarely glabrous, smooth; sepals not enlarged in fruit, columella triangular, c. 1.2 mm long. *Seeds* trigonous, c. 2 × 1 mm, covered with transverse striae that break up epidermis, striae radiating from hilum.

Distribution. Philippines (Luzon, Mindoro) and Sulawesi (Tenga, Utara, Minahassa, Pangkadyeu).

Habitat. This species was collected from fertile turf and dry riverbeds, but it is known only from few specimens in Sulawesi. In the Philippines it was collected also from coastal areas. Altitude: 10-600 m a.s.l. This species was found with flowers and fruits in February till June, but more specimens could expand on this as we saw now collections from later in the year than June.

Etymology. This species is named after the area where it was found as Celebes is the name formerly used for Sulawesi.

Notes

The collection *Koorders 16949* stored at Bogor herbarium (BO) is selected as lectotype, while additional specimens are stored in the Naturalis Biodiversity Center (L). The material at Bogor bears Koorders' handwriting and notes on comparisons with other species, making it likely that it was used in the first description by him (Koorders 1898). *Phyllanthus celebicus* agrees in almost all characters with *P. mindorensis* C.B.Rob., which was first described for the Philippines (Robinson 1909) and its distribution was expanded by Airy Shaw (1982) to include Sulawesi. Airy Shaw noted on material of *P. celebicus* that it was very similar to *P. mindorensis* and differences between the Koorders specimens and the description by Robinson (1909) only include minor qualitative differences. Pistillate flowers were dissected from specimens from the Philippines and Sulawesi previously assigned to *P. mindorensis* and these were found to have similarly lobed discs, but with slightly shorter lobes (c. 0.3 vs 0.6–0.7 mm). Taking into account the similarities in vegetative and floral characters and the variation shown by specimens from Sulawesi, we decided to synonymize *P. mindorensis* with *P. celebicus*.

Specimens examined. Indonesia, Sulawesi *W.H. de Vries s.n.* (L). Indonesia, Sulawesi, Minahassa, Manembo-Nembo *A.H.G. Alston 16549* (L). Indonesia, Sulawesi, Road Palu - Donggala, near Loli *M.M.J. van Balgooy 2976* (BO, L).

Indonesia, Sulawesi, Minahasa province (Menado), near Pinomorongan, near Kajoewatoe, *H.S. Koorders 16949* (BO, L). Indonesia, Sulawesi, Tengah, Palu *G.J. de Joncheere 1024* (L). Indonesia, Sulawesi, Utara, Tondano *E.A.Forsten* (L). Philippines, Luzon, Batangas prov., Mt. Lobo, *PNH (M.D. Sulit)15718* (L). Philippines, Luzon, Mt Arayat, *FB (H.M. Curran) 19333* (L). Philippines, Mindoro, Mt. Yagaw, *PNH* (*H.C. Conklin) 18674* (L). Philippines, Rizal Prov., *BS (M. Ramos) 731* (L). Philippines, Luzon, *BS (M. Ramos) 8194* (L).

2. *Phyllanthus minahassae* Koord.
Phyllanthus minahassae Koord., Meded. Lands Plantentuin 19: 588, 627 (Koorders 1898). — Lectotype (designated here): Indonesia, Sulawesi, Minahasa province, near camp Totok, Rata Totok, *S.H.Koorders 16954* (fieldnumber 2595) (lecto BO (BO1310079); isolecto L (L.2059450).

Shrubs, 1–2 m high, monoecious?, all axes pubescent with dark brown short stiff hairs; branching phyllanthoid; branchlets terete, 20–40 cm long, bearing 30–52 leaves, internodes 2–3 mm long. *Cataphyllary stipules* and *cataphylls* caducous, not seen. *Stipules* triangular, c. 1.5 × 0.3 mm, persistent, membranous, pubescent, base plane, margin brittle, apex acute. *Leaves* distichous; petiole c. 1.8 mm long, pubescent; blade elliptic, asymmetric, 2.6–4.1 × 1–1.7 cm, 2.4–3.4 times longer than wide, membranous to slightly coriaceous, pubescent, base cuneate, margin slightly thickened and flat, pubescent, apex acute-rounded to obtuse, mucronate, mucro 0.1–0.2 mm long, puberulous at base on lower side, glabrous on upper side, upper side darker green than lower side; venation pinnate, midrib flat on either side, lateral veins 4–6, indistinct. *Inflorescences* axillary fascicles, usually unisexual, staminate flowers up to 6 together, at basal part of branchlets, pistillate flowers solitary on distal part of branchlets. *Staminate flowers* c. 1.5 mm in diameter when closed, 3.3–4 mm when open; pedicel 1.3–4 mm long, terete, pubescent, thin; sepals 4, ovate, 1.5–1.6 × c. 1 mm, spreading, outside covered in short hairs, pale green, margin fimbriate and brittle, apex acute to attenuate, midrib indistinct; disc glands 4, alternating with sepals, oblong, 0.2–0.4 × 0.4–0.6 mm, indented from thecae; stamens 2, c. 0.4–0.5 mm high, filaments and connectives connate, staminal column c. 0.2 mm high, anthers slightly stipitate resulting in cross shaped connective, apically extended for 0.1–0.2 mm, thecae oblong, c. 0.3 × 0.2 mm, hanging above disc gland, dehiscing horizontally via slits. *Pistillate flowers* not seen, information derived from fruit; sepals 6, elliptic, enlarged (only in fruit?) to 14–16 × 5–6 mm, outside covered in short hairs, pale green, margin entire, pubescent, apex acute to obtuse, midrib indistinct; disc, ovary and stigmas not seen. *Fruits* capsules (already dehisced, only fragments on type), estimated at c. 6 mm in diameter and c. 6 mm high, minutely verrucate; pedicel terete, 3–4 cm long, puberulous; columella triangular, 4.8–6 mm long. *Seeds* trigonous, 4.2–4.8 × c. 2.2 mm, covered with transverse striae that break up epidermis, striae radiating from hilum.

Distribution. Known from two collections by Koorders from the same area in Sulawesi, Minahassa province.

Habitat. The label information of the type showed it to be common in forests on fertile vulcanic sand. It was found at c. 200 m a.s.l. Flowering and fruiting is in March, but this is only based on the type specimen and one additional collection around the same time.

Etymology. Named after the province where it was found on Sulawesi.

Notes. The lectotype is here selected from two collections by Koorders, both bear his handwriting, but only the specimen designated here as lectotype possesses remains of fruits and seeds. The staminate flowers were described from the other collection (*Koorders 16954*; BO1310078), but this specimen is in poorer condition, has less information on the label and has only dehisced fruits without seeds. *Phyllanthus minahassae* is probably closely related to *P. celebicus*, but it has larger leaves and very distinct pistillate sepals (at least in fruit). Large pistillate sepals are also found in the Indian species, *P. macrocalyx* Müll.Arg. (also subgenus *Eriococcus*) and some species of subgenus *Gomphidium* (Baill.) G.L.Webster (Schmid 1991), but there they actually enclose the fruit in development (Naveen Kumar et al. 2015).

Specimens examined. Indonesia, Sulawesi, Minahasa province, near camp Totok, Rata Totok *H.S. Koorders 16924* (fieldnumber 2430) (BO, L). Indonesia, Sulawesi, Minahasa province, near camp Totok, Rata Totok *S.H.Koorders 16954* (fieldnumber 2595) (BO, L).

Discussion

With the rather brief description of *P. celebicus* and *P. minahassae* by Koorders (1898), these two species could not be confidently assigned to any subgroup within *Phyllanthus*. By examining material collected by Koorders including his notes on the labels, we were able to place both species in subgenus *Eriococcus*. This subgenus is distributed in Asia (and one species in Australia) and its 4-merous staminate flower is a consistent character that can be used to identify them (Bouman et al. 2018). However, while the staminate flower offers more information on subgeneric placement, the pistillate flower is often more useful for species identification as found here for *P. celebicus* and *P. minahassae*. Subgenus *Eriococcus* is mainly known from mainland Asia (see Bouman et al. 2018), but only includes few species from Western Malesia (e.g. *P. acutissimus* Miq., *P. kinabaluicus* Airy Shaw, *P. singalensis* (Miq.) Müll.Arg.), which often have symmetric leaves (pers. obs.). Therefore, the species treated here are most likely closely related to other species from the Philippines, which also have asymmetric leaves that appear quite similar. Some species from the Philippines and Sulawesi of section *Eriococcus* seem to form a complex, all with usually pubescent axes, strongly asymmetric leaves and usually red flowers with fimbriate sepals (some exceptions occur). Other species that form this complex, aside from those already mentioned, include *P. laciniatus* C.B.Rob., *P. leytensis* Elmer, *P. sibuyanensis* Elmer, and perhaps *P. blancoanus* Müll.Arg. (see Robinson 1909). A thorough revision or phylogenetic study with sampling of these taxa might help to improve some of the species delimitations. This group of species could lend support to the inclusion of the Philippines in Wallacea (see van Welzen et al. 2011). While not many species of *Phyllanthus* occur on Sulawesi, the two species treated here already highlight the interesting flora found on the island and the need to study it further.

Acknowledgments
This work was done as part of the PhD research of the first author, funded by the Hortus botanicus Leiden and Leiden University. Travel funding granted by the Alberta Mennega foundation to visit herbaria in Indonesia and the Flora Malesiana symposium in Brunei is gratefully acknowledged. The directors and keepers of BO and L are thanked for use of their collections. Deby Arifiani and Michael Mambrasar are thanked for their help at BO herbarium with locating and studying the Koorders collections. Aninda Wibowo and Eka Iskandar helped with the abstract in Indonesian, for which we are very grateful. 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.

CHAPTER 6

Metabolic variation of selected *Phyllanthus* species and their correlation with antimicrobial activity

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Chapter 6

Metabolic variation of selected *Phyllanthus* species and their correlation with antimicrobial activity

Short title: Metabolic variation in *Phyllanthus*

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Abstract

The profiling of medicinal plants has resulted in the finding of many bioactive compounds with possible application in medicine, thereby also often confirming the basis of their pharmacological effects. The genus *Phyllanthus* has a long history of therapeutic history in Asia, South America and Africa, but the therapeutical species are limited to a few, mostly focusing on their antimicrobial activity. In this study, the metabolic profile of *Phyllanthus* species selected from several lineages was compared with each other to elucidate their active compounds. By correlating antimicrobial activity with the results from our profiling using Proton Nuclear Magnetic Resonance (H-NMR) spectroscopy, the results suggested that active compounds were most likely plant phenolics. The result of antimicrobial activity in liquid suspension indicated that *P. arbuscula, P. muellerianus, P. tenellus and P. urinaria* have significant activity on several gram-negative bacterial. Furthermore, *Phyllanthus fraternus* and *P. glaucus* also showed activity in initial agar-based assay, but this could not be confirmed in the liquid suspension. To identify the phenolics in detail, subsequent investigation using a targeted approach with high performance thin layer chromatography (HPTLC) showed that the active species differed in the profile of plant phenolics.

Keywords: antimicrobial, Phenolics, Phyllanthaceae, *Phyllanthus*, high performance thin layer chromatography

Introduction

Natural products have been for long time the most plentiful resource for bioactive or nutritive chemicals utilized in pharmaceutics, cosmetics, foods and agriculture

(Koehn & Garter 2005; Harvey 2008; Cragg & Newman 2013; Newman & Cragg 2016). While recently more diverse natural products are starting to be used as a resource for novel medicines, including microbes, insects and marine organisms (Cragg & Newman 2013), plants still represent the most sustainable options, particularly with a long history of their utilization. However, the use of natural products does present some difficulties, which include issues with sustainable access and supply, discussions on intellectual property rights, the difficulty of extracting a single active compound from the extracted mixtures and finally the slowness in getting new agents to the market (Koehn & Garter 2005; Harvey 2008; Wu & Chappell 2008; Yuliana et al. 2011). Botanical gardens harbour a large diversity of rare plants and are a valuable source for the plant sciences (Shan-An & Zhong-Ming 1991; Faraji & Karimi 2020). Based on the results of recently developed metabolomics, many influential factors on the metabolome could be deduced including the genotype, developmental stage and environmental or external factors (Jahangir et al. 2008; Kim et al. 2011). Not only chemical profiling but also, the correlation between metabolome and bioactivity against bacteria, fungi and viruses has received great attention in the field of metabolomics applications. Previously, there have been many similar approaches, a Mexican medicinal plant, *Gaphimia glauca* Cav., was investigated for its sedative triterpenoids (Cardoso-Taketa et al., 2008). In the study, a wide range of the accessions of the plants were measured for their sedative activity and correlated with the metabolome detected by ^{1}H NMR. In addition, some methoxy flavonoids of *Orthosiphon stamineus* Benth. were found to be responsible for Adenosine A1 receptor binding activity by similar ^{1}H NMR-based metabolomics (Yuliana et al., 2011).

Phyllanthus L. is a large genus with more than 800 species that occurs in all tropics and subtropics (Govaerts et al. 2000; Bouman et al. 2018). Several species have a long history in traditional medicine and are used for several purposes (see Unander et al. 1990; Calixto et al. 1999). Some species are well known, such as *P. emblica*, whose fruits are usually used for their high nutritional content like vitamin C (Masuma et al. 2014; Hasan et al. 2016; Yadav et al. 2017; Lanka 2018). However, most of them are common herbs that are often invasive and therefore have a wide distribution, which might pose interesting questions on differences in activity per locality (see Cardoso-Taketa et al. 2008). Not only are the species used in medicine or as healthy foods, but some species are also known to be used as fish poison in South America (Patiño 1967; van Andel 2000; Neuwinger 2004; Webster 2003).

The interest in *Phyllanthus* has sparked a great number of studies, which has resulted in more than 500 reported compounds that have been extracted from *Phyllanthus* (Mao et al. 2016). *Phyllanthus* species have been found to be very rich in alkoloids, flavonoids, lignans, tannins and triterponoids (Calixto et al. 1999; Mao et al. 2016). Several studies have focused on testing the medicinal effects of *Phyllanthus* and most studies focus on anti-viral effects (Thyagarajan et al. 1988; Barrio & Parra 2000; Liu et al. 2001; Alvarez et al. 2009). The medicinal effects of many *Phyllanthus* species have also been demonstrated in some studies that tested against bacteria (Bagalkotkar et al. 2006, Jagessar et al. 2008, Mehta et al. 2014) and fungi (Agrawal et al. 2004). The most interesting application is the activity against hepatitis B using *P. amarus* (Yeh et al. 1993; Thyagarajan et al. 1998; Patel et al. 2011) and *P. niruri* L. (Venkateswaran *et al.* 1987; Thyagarajan *et al.* 1988; Yeh *et al.* 1993; Wang et al. 1995; Lee et *al.* 1996; Wu *et al.* 2015; Kamruzzaman & Hoq 2016).

Closely related species of plants may generally have a similar chemical profiling that might results in similar pharmacological activity with some degree of difference (e.g. Beara et al. 2012). However, in the case of *Phyllanthus* species, compared with other species, the applications of individual species greatly differ from each other, which could propel a detailed study of chemical profiling to cover a broad range of metabolites and the metabolome.

In the past, with the advancement of metabolomics tools, many analytical platforms have been applied to the metabolomics of plants for many purposes e.g., deconvolution of physiological phenomena, chemical taxonomy, and agricultural applications (Choi et al. 2004; Kim et al. 2010a; Kim et al. 2010b). Moreover, a metabolomics tool has been applied in the chemical comparison of a few *Phyllanthus* species (e.g. Mediani et al. 2005; Wang et al. 2011), but has not yet been applied to a larger number of species. To study the metabolome of these species, ^{1}H NMR was chosen to get information on more groups of metabolites. However, for longer term projects, a fingerprinting approach is required together with the identification of minor compounds.

Previous studies indicated that several species of Phyllanthus might be interesting for their antimicrobial activity. In this study we aim to compare the metabolic profile and potential anti-bacterial and anti-fungal activity of various *Phyllanthus* spp. from different lineages or geographical areas. Using a diverse selection of species ranging from herbs to shrubs and small trees, some of which with known traditional medical applications we hope to further explore the basis of their medicinal effects and to test these species for bioactive compounds.

Methods

Plant material

Fresh material of all plants used in this study were collected from the Hortus botanicus Leiden (Leiden, The Netherlands). The plants originated from different geographic areas, but were all grown at the botanical garden under similar growing conditions. Eleven species of *Phyllanthus* that cover a high degree of the variety within the genus were selected, including a few often used in traditional medicine. The age of the selected plants varied depending on the type of lifestyle such as annual herbs, shrubs and one aquatic species. Most of species were collected with three replicates to remove biological variation except for the large species of shrubs (e.g., *P. arbuscula*, *P. juglandifolius*, *P. glaucus*). Samples were taken several times during the span of a year. In total 27 samples from 11 species were selected for the study (table 6-1).

Preparation of plant samples for metabolomics analysis.

Collected materials were stored in the freezer at -80°C before processing. Materials were ground to a fine powder with mortar and pestle under liquid nitrogen and then transferred to a 50 ml tube and subsequently placed in a freeze drier for 72 hours.

^{1}H NMR experiments

For ^{1}H NMR screening, 20 mg of freeze-dried plant material was extracted with 1 mL of a mixture of CH_3OH-d_4: KH_2PO_4 buffer in D_2O (1:1, v/v, pH 6.0) containing 0.29 mM trimethylsilane propionic acid sodium salt (TMSP). The extracts were vortexed and subsequently sonicated for 20 minutes and then centrifuged at 13,000 rpm for 10 minutes. A volume of 300 µl of the supernatant of each extract was transferred to 3mm-NMR tubes. ^{1} H NMR spectra were recorded at 25 °C on a 600 MHz Bruker AV 600 spectrometer (Bruker, Karlsruhe, Germany) equipped with cryo-probe operating at a proton NMR frequency of 600 MHz. The methyl signal of CH_3OH-d_4 was used as the internal lock. Each ^{1}H NMR spectrum consisted of 64 scans requiring 5 min acquisition time with the following parameters: 0.25 Hz/point, pulse width (PW) = 30° (10.8 s), and relaxation delay (RD) = 1.5 s. A pre-saturation sequence was used to suppress the residual H_2O signal with low power selective irradiation at the H_2 O frequency during the recycle delay. Free induction decays (FIDs) were Fourier transformed with Line Broadening (LB) = 0.3 Hz and the spectra were zero-filled to 32 K points. The resulting spectra were manually phased and baseline corrected and calibrated to Theory of Spectroscopy and Molecular Properties (TMSP) at 0.0 ppm, using TOPSPIN (version 3.0, Bruker).

High performance thin layer chromatography (HPTLC) and Liquid chromatography–mass spectrometry (LC-MS)

The metabolites of *Phyllanthus* species were further analysed by high performance thin layer chromatography (HPTLC). The results were compared between active and nonactive samples and used in further antimicrobial activity testing against *Staphylococcus aureus* Rosenbach. HPTLC chromatographic separation was performed on 20 x 10 cm HPTLC silica gel F_{254} plates (Merck, Darmstadt, Germany) and samples were applied using an automatic Thin Layer Chromatography (TLC) sampler (CAMAG, Muttenz, Switzerland). For chemical profiling, we applied 15 µl while 35 µl was applied for the bioautography tests from 2 mg/ml methanol extracts. The band length was 6 mm for each sample, and they were spaced 10 mm from the bottom of the plate and 20 mm from the left and right border of the plate. The distance between tracks was 18 mm allowing for 9 samples to be spotted on each plate. To separate non-polar compounds, the mobile phase consisted of toluene-ethyl acetate (8:2, v/v). For polar compounds separation, a mixture of ethyl acetate-formic

Table 6-1. List of samples of each species included in this study, for each species the subgenus, habit and life stage is noted along with the Registration number of the Hortus botanicus Leiden.

Sample nr	**Species**	**Subgenus**	**Habit**	**life stage**	**Hortus number**
ARB01	*P. arbuscula* (Sw.) J.F.Gmel	*Xylophylla*	Shrub	Non-flowering	HBLA00587-02610
ARB02	*P. arbuscula* (Sw.) J.F.Gmel	*Xylophylla*	Shrub	Non-flowering	HBLA00587-02610
FLU01	*P. fluitans* Benth. Ex Müll.Arg.	*Isocladus*	Aquatic herb	Non-flowering	HBL20150681
FLU02	*P. fluitans* Benth. Ex Müll.Arg.	*Isocladus*	Aquatic herb	Non-flowering	HBL20150681
FLU03	*P. fluitans* Benth. Ex Müll.Arg.	*Isocladus*	Aquatic herb	Non-flowering	HBL20150681
FRA01	*P. fraternus* G.L. Webster	*Swartziani*	Herb	Flowering	HBL20160134
FRA02	*P. fraternus* G.L. Webster	*Swartziani*	Herb	Flowering	HBL20160134
FRA03	*P. fraternus* G.L. Webster	*Swartziani*	Herb	Flowering	HBL20160134
GLA01	*P. glaucus* Jabl.	*Kirganelia*	Shrub	Non-flowering	HBL20160136
JUG01	*P. juglandifolius* Willd.	*Xylophylla*	Shrub	Non-flowering	HBL20170041
MIR01	*P. mirabilis* Müll.Arg.	*Phyllanthodendron*	Shrub	Non-flowering	HBL20090748

MIR02	*P. mirabilis* Müll.Arg.	*Phyllanthodendron*	Shrub	Non-flowering	HBL20090749
MUE01	*P. muellerianus* (Kuntze) Exell	*Kirganelia*	Herb	Non-flowering	HBL20160132
MUE02	*P. muellerianus* (Kuntze) Exell	*Kirganelia*	Herb	Non-flowering	HBL20160132
MUE03	*P. muellerianus* (Kuntze) Exell	*Kirganelia*	Herb	Non-flowering	HBL20160132
PEN01	*P. pentandrus* Schumach. & Thonn	*Tenellanthus*	Herb	Budding flowers	HBL20160133
PEN02	*P. pentandrus* Schumach. & Thonn	*Tenellanthus*	Herb	Budding flowers	HBL20160133
POL01	*P. polyspermus* Schumach.	*Kirganelia*	Herb	Non-flowering	HBL20160135
POL02	*P. polyspermus* Schumach.	*Kirganelia*	Herb	Non-flowering	HBL20160135
POL03	*P. polyspermus* Schumach.	*Kirganelia*	Herb	Non-flowering	HBL20160135
TEN01	*P. tenellus* Roxb.	*Tenellanthus*	Herb	Flowering	HBL20140316
TEN02	*P. tenellus* Roxb.	*Tenellanthus*	Herb	Flowering	HBL20140316
TEN03	*P. tenellus* Roxb.	*Tenellanthus*	Herb	Flowering	HBL20140316
URI01	*P. urinaria* Beille	*Emblica*	Herb	Flowering	HBL20140356
URI02	*P. urinaria* Beille	*Emblica*	Herb	Fruiting	HBL20140356
URI03	*P. urinaria* Beille	*Emblica*	Herb	Fruiting	HBL20140356

acid-acetic acid-water (100:11:11:27, v/v/v/v) was used. A saturation time of 20 min was set for all chromatographic separations and the solvent migration distance spanned 85 mm from the application point. The plate images were recorded using a TLC visualizer (CAMAG) under 366 nm UV light.

The samples were analysed using liquid chromatography mass spectrometry (LC-MS) using a UHPLC-DAD-QTOF, Thermo Scientific (Dreieich, Germany) UltiMate 3000 system coupled to a Bruker (Bremen, Germany) OTOF-Q II spectrometer with electrospray ionization (ESI). The mass spectrometer parameters were set as follows: nebulizer gas 2.0 bar, drying gas 10.0 mL/min, temperature 250°C, capillary voltage 3500 V. The mass spectrometer was operated in positive mode with a scan range of 100 – 1650 m/z, and sodium formate was used as a calibrant.

Bioassays

We screened for general antifungal activity for each plant species and this a was conducted by paper diffusion assay against *Fusarium oxysporum*. To produce spores, two weeks old plates were filled with 25 mL of sterile physiological solution (PS), then the media plates was rubbed with a sterile cotton swab to transfer spores to the PS. After that, the liquid containing the fungal structures was recovered with a sterile pipet and filtered through two layers of sterile miracloth and transferred into a sterile 50 mL-centrifuge tube. The volume was adjusted to 30 mL with sterile water, vortexed for 15 seconds and centrifuged at 4000 rpm for 10 minutes. This process was repeated three times. The supernatant was discarded, and the pellet was re-suspended in 30 mL of sterile PS. After, spore concentration per milliliter was quantified in a cell counter apparatus (Bio Rad). Potato dextrose agar (PDA) was sterilised and cooldown to 60 °C. Then 49 mL of PDA were inoculated with 1 mL of the spore solution and softly homogenized. The final spore concentration in the medium was 2.5×10^5 spores/ml. The treatments were sterile 6 mm paper discs loaded with 500 µg of methanol extract. In order to eliminate the methanol from the discs, after loading they were dried at room temperature for 5 min. The negative control consisted of a sterile disc paper with and without methanol processed in the same way of the plant methanol extracts. The plates were incubated at 28 °C for 39 hours and the diameter of inhibition zones were recorded.

Each sample showed mild activity against *Fusarium oxysporum*, but effectivity was low in general, so we opted to do further testing for antibacterial effects instead. For the first test, one hundred mg of dried material was extracted with 10 ml of methanol using ultrasonicator for 30 minutes at room temperature. 10 ml of *n*-hexane was added to remove chlorophyll which may hinder the biological activity. After hexane fraction was discarded, remaining extracts were further evaporated using rotary evaporator. Extracts were transferred to 1.5mL-microtube tubes after re-dissolving them in 1 mL MeOH, and dried completely by Speed-vac.

In the first test, the antimicrobial activity was tested using the disc-

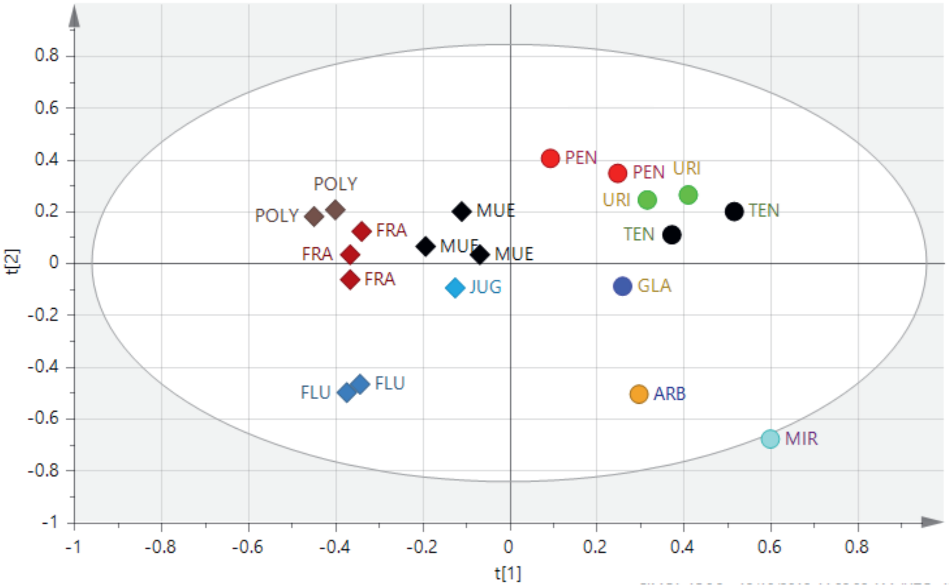

Figure 6-1. PCA score plot of NMR data, Sample names are shorted from table 1.

diffusion methods against *Bacillus subtilis* (gram positive) and *Escherichia coli* (gram negative). Unfortunately, only 20 of the extracts had sufficient material after ^{1}H NMR screening for the bioassay test. The test was performed as described in previous studies (Abreu et al. 2014). All extracts were prepared in MeOH. Each extract was added to previously autoclaved and cooled LB agar in the amount calculated to obtain the required final concentration of 500 ug. Then, 20 mL of medium was poured into 90 mm Petri dishes. The bacterial suspensions were adjusted to 0.5 McFarland standard and seeded over hardened LB agar Petri dishes using a sterilized cotton swab. Sterile blank discs (6 mm diameter; Oxoid) were placed on the agar plate seeded with the respective bacteria. The plates were incubated at 37 °C for 24 h. After incubation, each inhibition zone diameter (IZD) was recorded and analyzed according to CLSI guidelines (reference above). The results were correlated with the NMR spectra as described below to determine the class of compounds we should focus on.

In the second test, we tested one sample of each species in concentrations of 125, 250 and 500 µg/ml against *B. cereus* strain NCCB 75009, *B. subtilis* strain *168* and *S. aureus* strain ATCC29213 to corroborate the bioactivity of each species of *Phyllanthus*. This was done using concentrations of 125, 250, 500 or >500 µg/ml of dried extracts in 100% MeOH (MIC testing). Dissolved extracts from each concentration was incubated in a liquid medium containing the tested bacteria. To determine the specific compounds underlying the bioactivity of the species

Nr	Sample name	Bacteria Gram +	Bacteria Gram -	Fungal
1	ARB01			
2	URI01	+		
3	JUG01			+
4	FRA03	++	++	+
5	FLU03			
6	MUE02	+		
7	TEN03	++		+
8	URI02	+		+
9	ARB02			+
10	MIR02			
11	MUE03	+		
12	GLA01	++	+	+
13	FRA01			+
14	POLY01			
15	URI03	+	++	
16	FRA02			+
17	TEN02	+		
18	FLU02			+
19	MUE01	++	++	
20	POLY02			

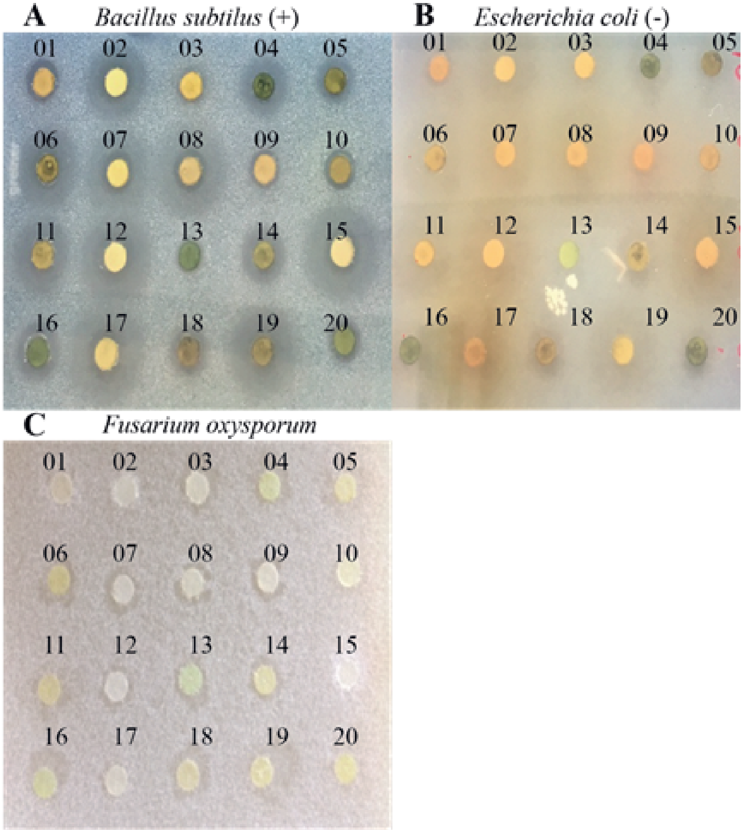

Figure 6-2. Bioactivity testing of various *Phyllanthus* spp. Extracts listed on the left by sample names with results from bioactivity screening against a gram positive bacteria, gram negative and a fungus strain, activity is only shown when mild (+) or strong (++) activity was recorded. On the right is shown the results from the disc diffusion method for A) against the gram positive bacteria *Bacillus subtilis* (+), B) against *Escherichia coli* and C) against *Fusarium oxysporum*.

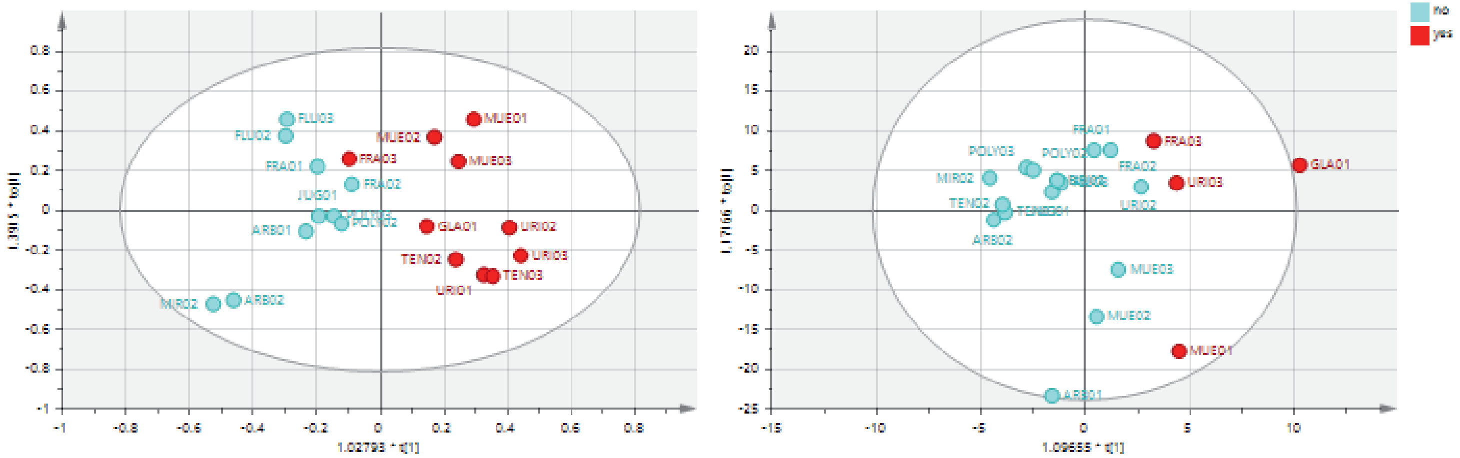

Figure 6-3. OPLS-DA plot of activity test against *Bacillus subtilis* (left, Q2 is 0.526, CV-ANOVA: P=0.0183117) and *Escherichia coli* (right, Q2: -0.308, CV-ANOVA: P=1).

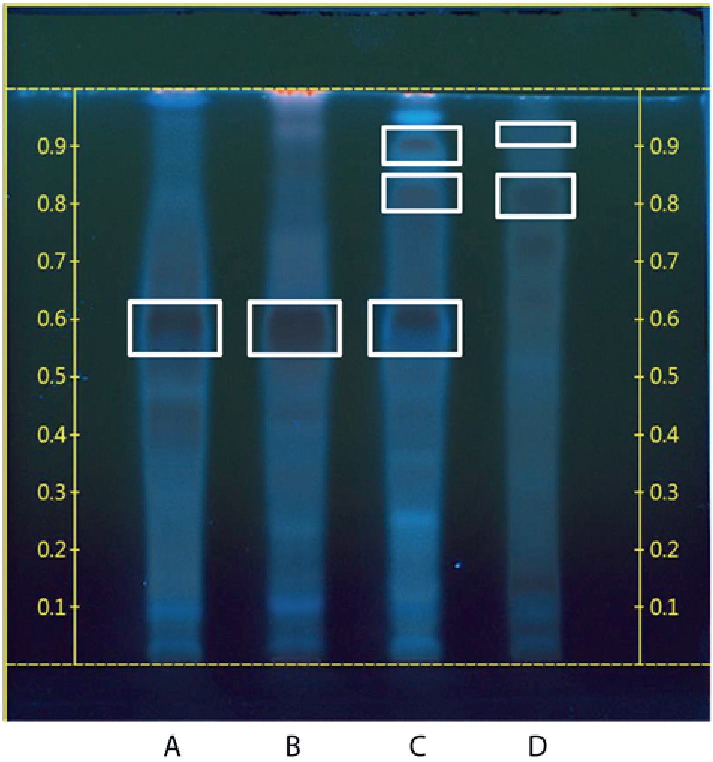

Figure 6-4. Bioautography with the HPTLC spectra of selected species of *Phyllanthus* screened for activity against *S. aureus*. From left to right, the species is *P. urinaria* (A), *P. muellerianus* (B), *P. tenellus* (C) and *P. arbuscula* (D), active bands extracted for LC-MS in the spectra are highlighted with white boxes.

resulting from test two, we applied in the third step direct testing with a 0.5 McFarland solution of *S. aureus* that was sprayed on a HPTLC plate following preparations described below. The plates were incubated for 24 hours and checked afterwards for activity under UV light.

Data processing and multivariate data analysis for metabolome and activity correlation

Spectral data was bucketed using the AMIX program ((Bruker Biospin Corp., Billerica MA), bucket size was 0.04 ppm and the areas were normalised to total intensity. Intervals for methanol and water signals were deleted from the bucket data. Multivariate data analysis was performed using SIMCA-P V.14.1 (Umetrics, Umeå, Sweden). Differentiation of the various *Phyllanthus* species was shown using Principal Components Analysis (PCA) and orthogonal partial least square discriminant analysis (OPLS-DA) and of the ^{1}H NMR data. The samples were divided in two classes for Y-variables in OPLS modeling. PCA and OPLS-DA analysis data was scaled using the Pareto and unit-variance (UV) scaling method.

Results

Principal component analysis (PCA)

Principal component analysis (PCA) showed a good separation for each species (Fig. 6-1), but the closeness between species did not follow the previous morphological and genetic data. The top-right corner does show three of the four herbaceous species, but *P. fraternus* places more closely to some shrubs and small trees from Africa and South America. No clear pattern related to evolution, morphological adaptation or habitat in the greenhouses are evident from the PCA plot.

Biological activity testing

Initial activity testing for anti-fungal properties against *F. oxysporum* showed low activity for most species, but none of the samples showed a particular strong reaction against the fungi. Strongest activity was seen in all tested samples of *P. fraternus*, but testing of other species like *P. urinaria* only showed mild activity in one of the samples. As our anti-fungal testing were largely inconclusive with only mild activity in some species, we opted to do further screening for antibacterial testing instead.

Activity testing against the gram-negative bacteria *E. coli* and the gram-positive bacteria *Bacillis subtilis* (Fig. 6-2a and b) showed more active species against the latter (Fig. 6-2a and b). During testing against pathogenic fungi, *P. fraternus* showed a mild activity against *Fusarium*. Some other species showed some activity against *Fusarium*, but this was not always consistent for each extract of a specific species. As the plate did not show particularly strong activity as it did not show a significant correlation in the OPLS-DA (not shown here), we continued with the anti-bacterial bioactivity in the following steps. Extracts were divided into two classes, active and non-active, to discriminate metabolites, that were more involved in the antibacterial or antifungal activity. Correlating antimicrobial activity with the ^{1}H NMR data using OPLS-DA was not significant against *B. subtilis* strain *168*, but not validated (P=0.0183117; Q2 = 0.526). The significant p-value indicates some biological effect, but to improve the Q2 value, we would need to increase the sample size. Figure 6-3 shows a good separation of active (red) and non-active (blue) species. In the case of *E. coli*, the extracts of *P. urinaria* and *P. muellerianus* showed some inhibition, but the separation between active and non-active was not validated by OPLS-DA (Fig. 6-3 right). Subsequent testing against more gram-positive bacteria showed the strongest activity against *S. aureus* and this was selected for further testing using HPTLC to isolate the compounds that could possibly have caused the anti-microbial effects.

Targeted approach (HPTLC/LC-MS) for compound identification

Samples showed a good separation of bands on the HPTLC profile which were largely similar, but only the extracts run on a polar phase showed some reaction to *S. aureus*. Activity was tested with both TLC plates using the direct spray method. The non-polar compounds did not show any activity, but some polar compounds showed antimicrobial effects (Fig. 6-4). Due to unavailability of more material from test 1, only a limited number of species could be tested with the HPTLC and four are shown in figure 6-4. We targeted these for identification using HPTLC coupled with LC-MS, but only one compound could be identified. The highest peak in the LC chromatogram profile of *P. tenellus* were cross referenced with Buckingham (1993) and indicated flavan-like compounds, but we could not identify other possible fragments due to the low concentration of the extracts.

Discussion

The medicinal value of *Phyllanthus* has become a field of high interest (Kuttan & Harikumar 2011; Mao et al. 2016). Many species were already known to have some medicinal effect from traditional medicines (Unander et al. 1990, 1991, 1992, 1995). In this study, several methods were combined to elucidate the potential antimicrobial effect of a few species commonly found in botanical gardens or as invasives. These were also aimed at sampling a larger morphological variety within *Phyllanthus* instead of focusing on any specific taxon. Proton NMR is a strong tool to study the metabolome and it indicated that phenolics were an important class of compound when it was correlated with activity (Fig. 6-2). Our correlation of activity and the NMR data was used as a tool to predict the active compounds as it has been used before (Eriksson et al. 2006). Accessional differences as shown by figure 6-2 were present within our samples, as antimicrobial activity was not always at the same level between extracts. This was also indicated in the initial general antifungal screening, but the effects were quite low. Our study did not manage to identify all compounds attributed to the antimicrobial effects detected in some species. Only small indications were found for flavan in *P. tenellus*, which has been found before in this species (Buckingham 1993). Several issues could underlie our inability to identify the remaining compounds. This includes a strong adherence to the plate silica that prevented them from separating well in the TLC, or it is a matter of concentration of the extracts. The strength of activity against *S. aureus* (Fig. 6-4) was also different from the initial tests with *E. coli* (Figure 6-2), possibly due to differences in testing method, solvent, or the age of the extracts. The results presented here are quite fragmented as material was not available for all experiments, so future studies would need to gather more fresh material for a more thorough screening of *Phyllanthus*.

While our approach was unable to identify the antimicrobial compounds in this study, similar research has generated a wealth of knowledge on the bioactivity of other species. Ghafar et al. (2020) similarly used H-NMR coupled liquid chromatography in *P. acidus* to identify almost 80 compounds, some of which were involved with antioxidant, anti-diabetic and anti-inflammatory reactions (see also Muthusamy et al. 2017). Of the species from this study, especially the three annual herbs *P. urinaria*, *P. fraternus* and *P. tenellus* are good candidates for their medicinal value due to their rapid growth. Over 90 naturally occurring compounds have been reported for *Phyllanthus urinaria* (Fang et al. 2008; Geethangili & Ding 2018), many of which were shown to have an antioxidant effect.

While the genus *Phyllanthus* with almost 900 species (Bouman et al. 2018) has a long history in traditional medicine, the majority of studies have focused on a few select species, especially more common herbaceous species like *P. urinaria* (Geethangili & Ding 2018), *P. niruri* (Kamruzzaman & Hoq 2016) and *P. amarus* (Patel et al. 2011). In this study we attempted to include a broader variety of species of various habits, countries of origins and across the phylogeny of the genus. Unfortunately, due to sampling issues and inconsistent results of bioactivity screening, we were unable to elucidate any compounds with antimicrobial activity. Some activity was found in a few species and future studies might improve upon our work to find those compounds of interest for their medicinal value.

CHAPTER 7

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

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

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

Chapter 7

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

Short title: Phylogenetics of the genus *Phyllanthus*

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Abstract

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

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

Introduction

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

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

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

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

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

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

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

Materials and methods

Taxon sampling

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

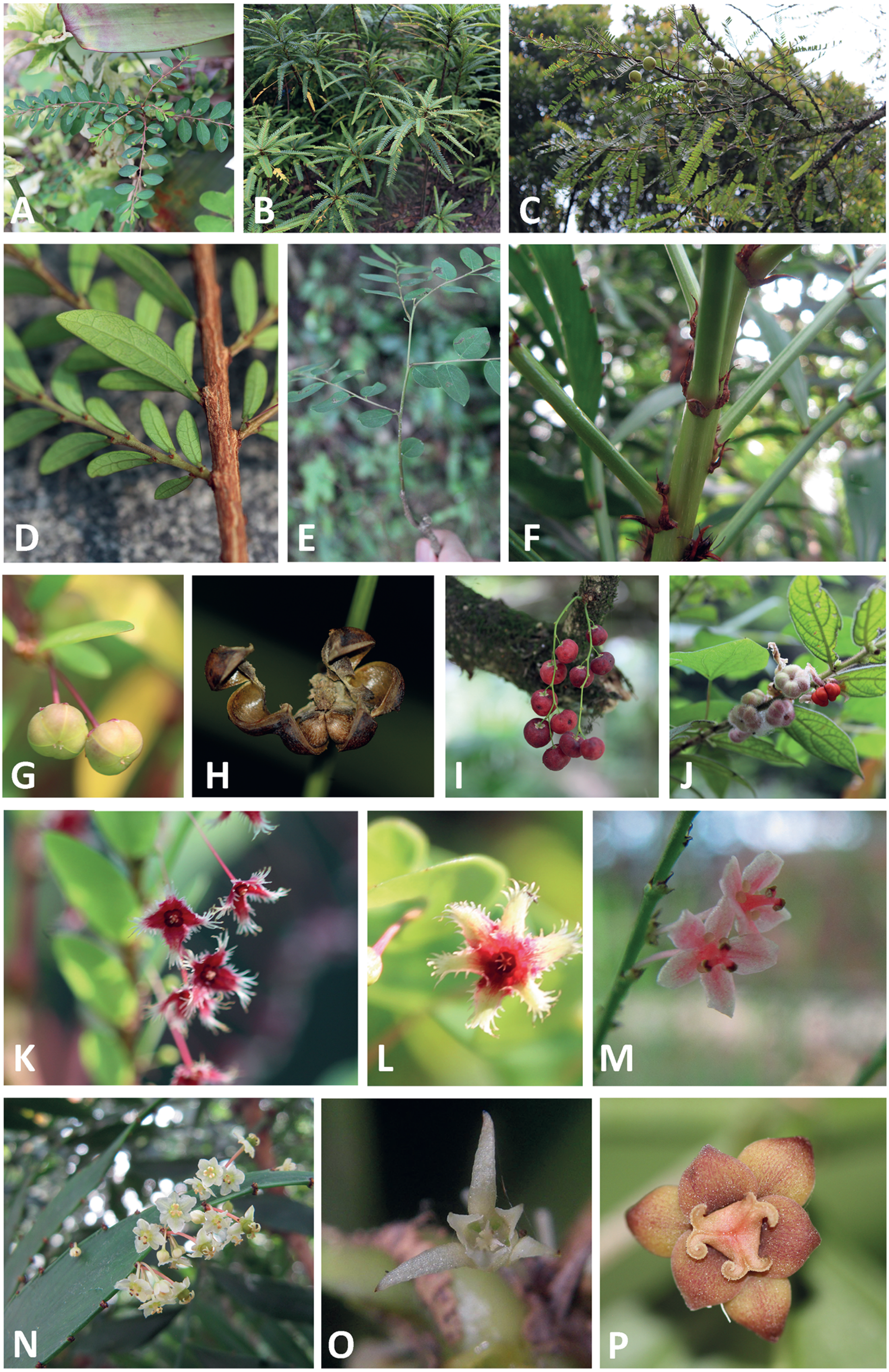
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Figure 7-1. Major characters of *Phyllanthus* and related genera *Breynia* and *Glochidion*. A. habit of the herbaceous *P. tenellus* (subgenus *Tenellanthus*); B. habit of *P. watsonii* (subgenus *Eriococcus*); C. habit and fruits of *P. emblica*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

DNA extraction, amplification and sequencing

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

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

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

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

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

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

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

Sequence cleaning, alignment and resulting datasets

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

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

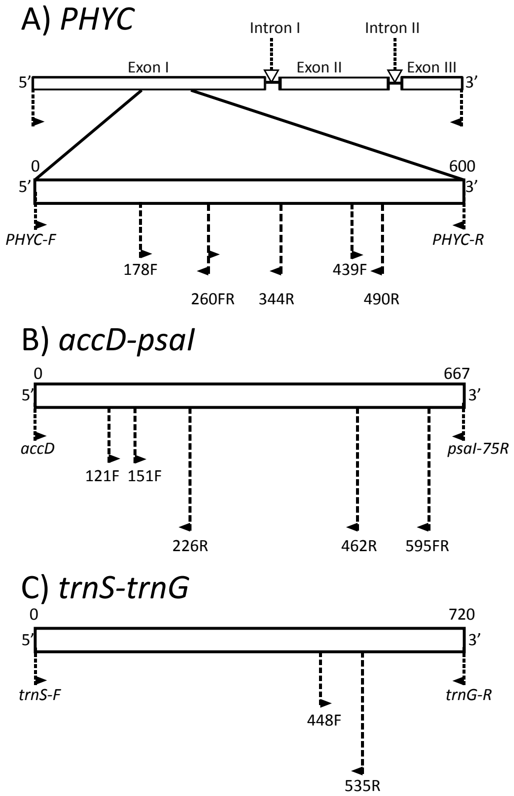


Figure 7-2. Schematic design for the spacer *PHYC* (A), *accD–psaI* (B) and *trnS–trnG* (C) spacer with newly designed primers indicated by arrowheads. Number behind primer names indicates approximate nucleotide position within the marker including insertions in the matrix. *PHYC* figure adapted from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

Phylogenetic analyses

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

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

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

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

Results

Analysis of the individual and combined nuclear/combined chloroplast markers

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

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

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

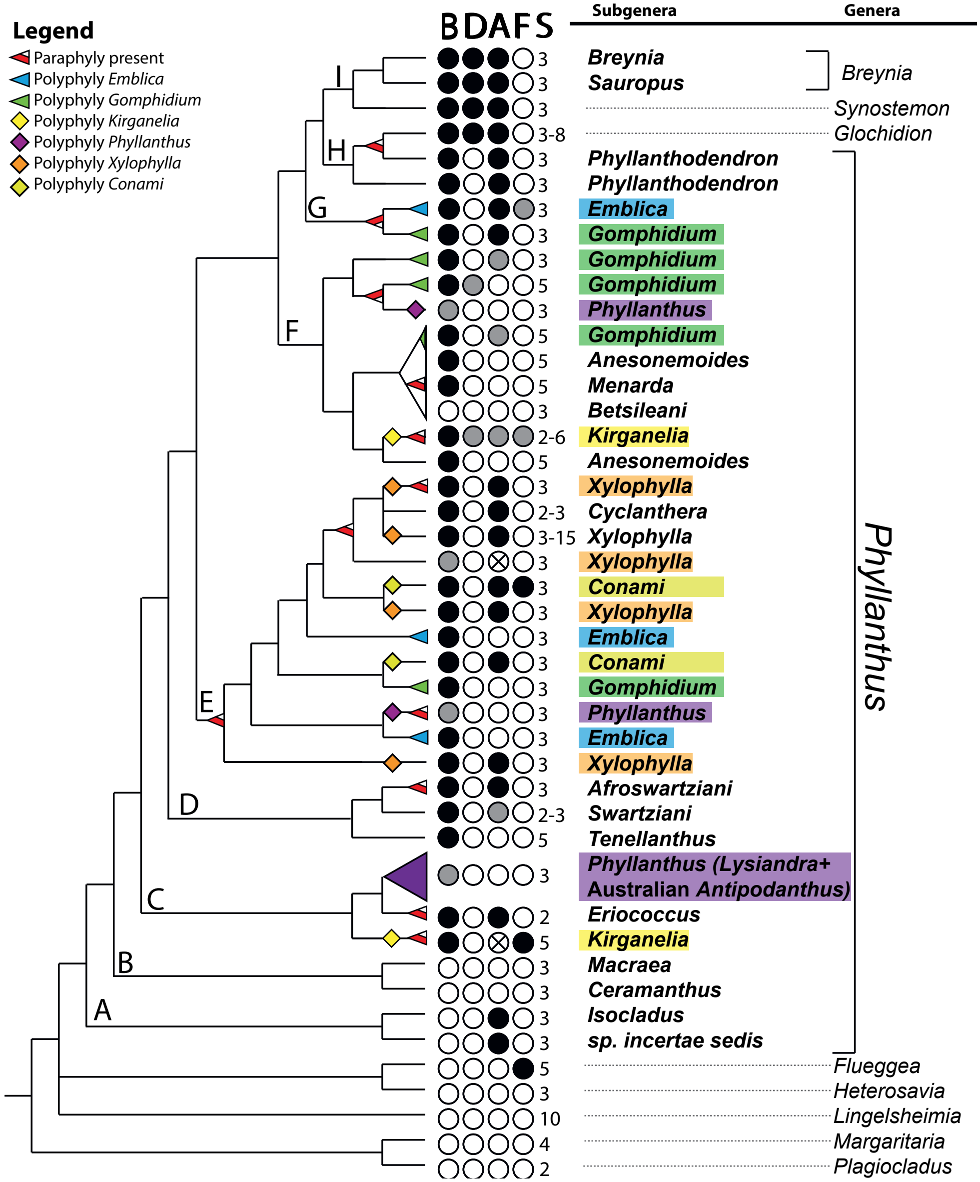


Figure 7-3. Molecular phylogenetic relationships of tribe Phyllantheae, simplified from Fig. 7-4 showing genera and subgenera. Colouring of clades follow Fig. 7-4 and paraphyly is highlighted with a red triangle (◀). Several morphological characters and character states are shown: (B) branching non-phyllanthoid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

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

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

Discussion

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

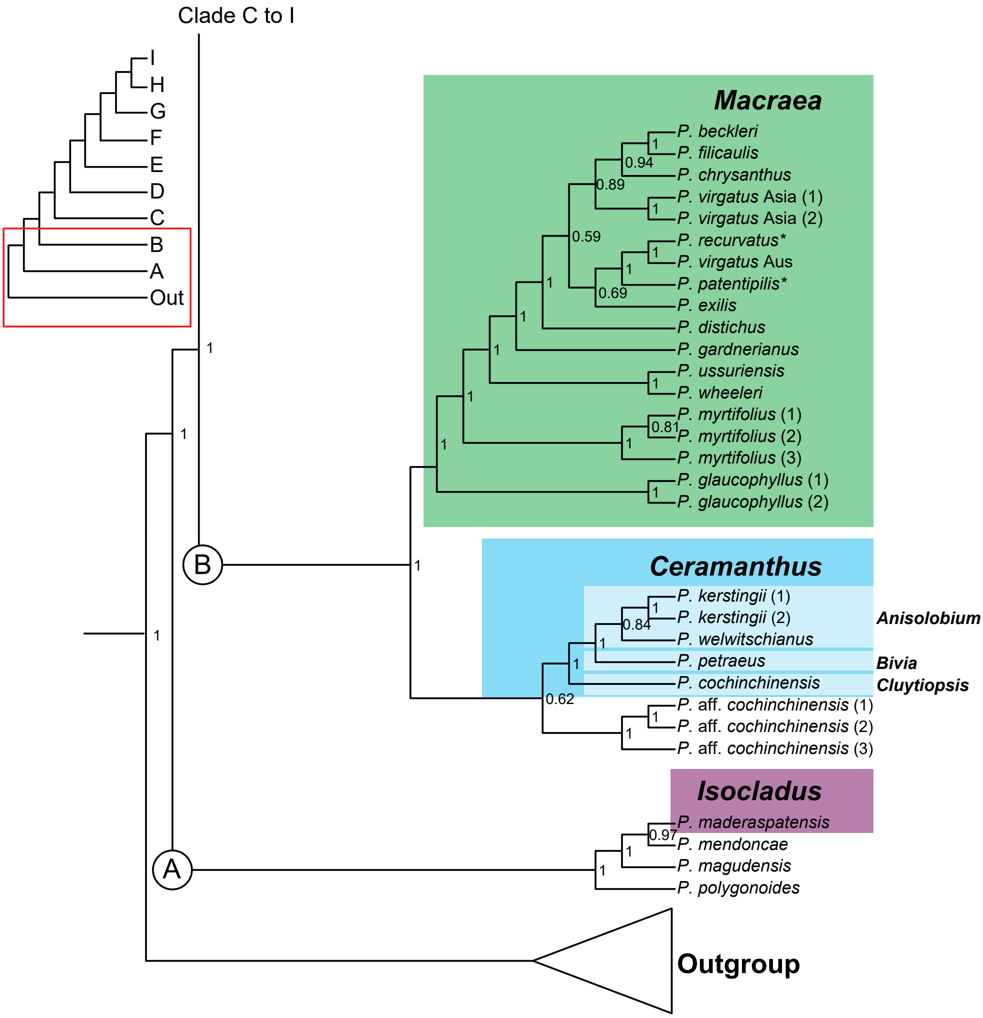
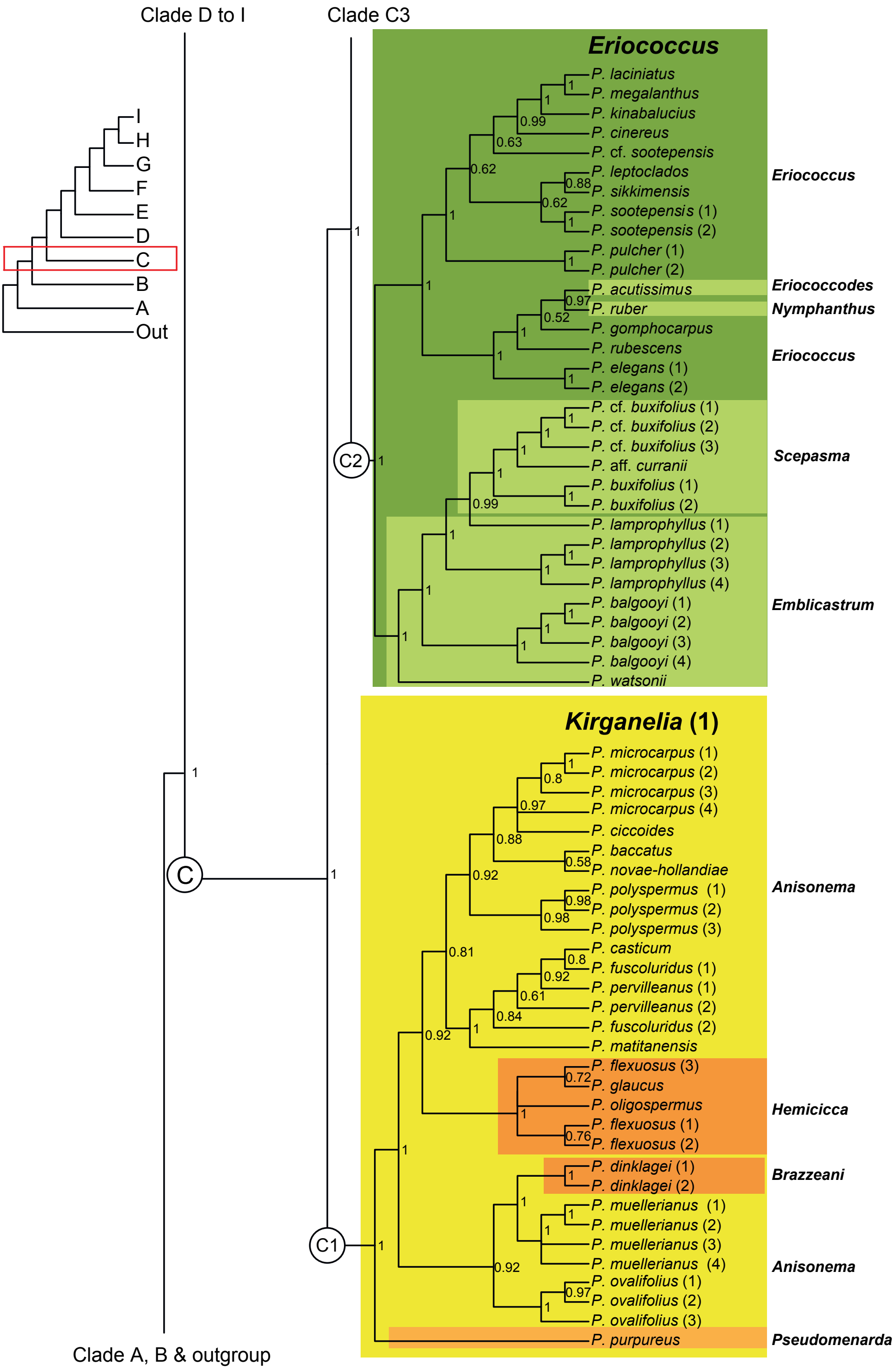


Figure 7-4. Bayesian majority rule consensus tree of the full combined nuclear (ITS and *PHYC*) and chloroplast (*accD–psaI*, *matK* and *trnS–trnG*) datasets for *Phyllanthus* and related genera, posterior probabilities (PP) are displayed at the nodes, infrageneric classification follows Bouman *et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


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

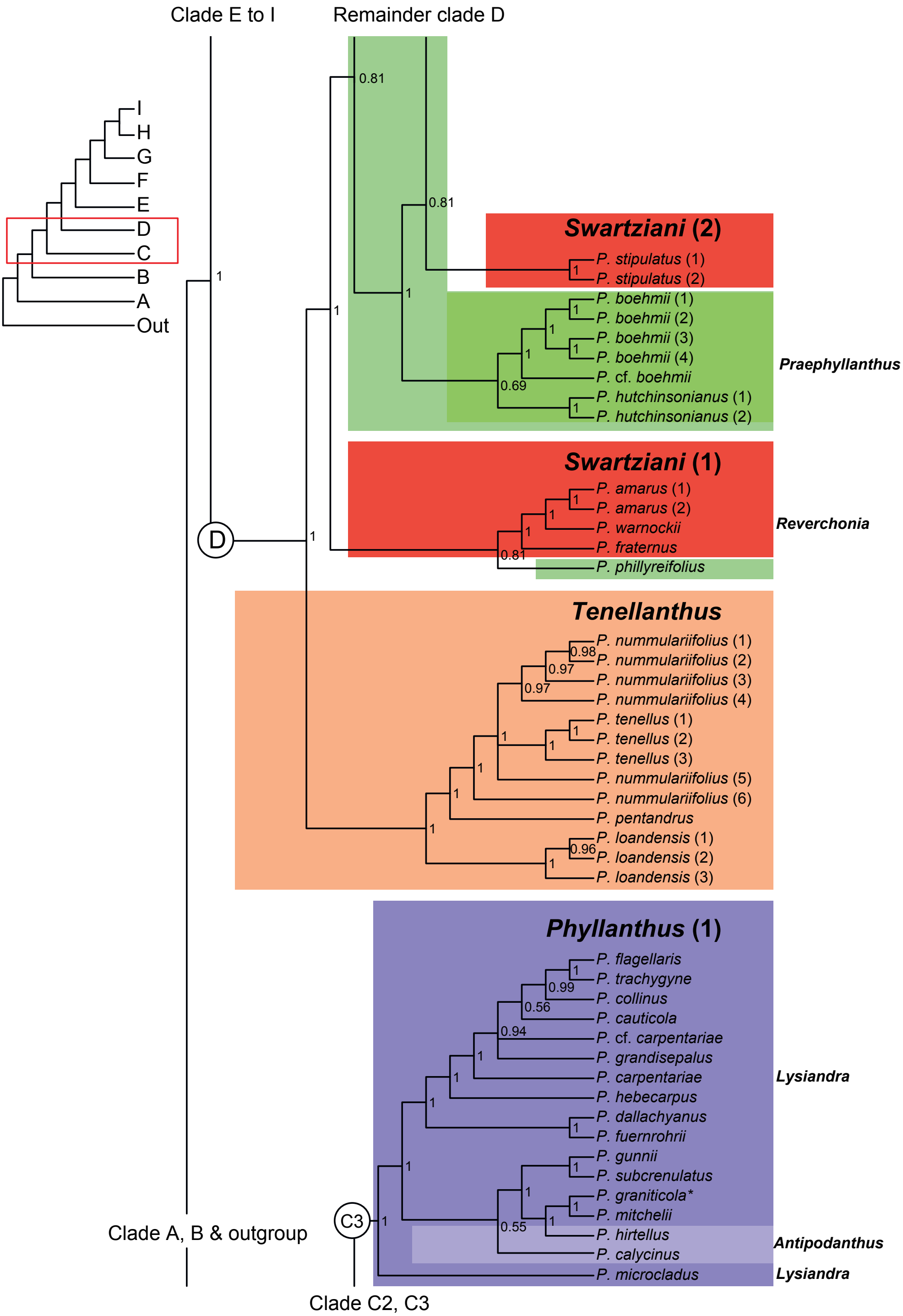
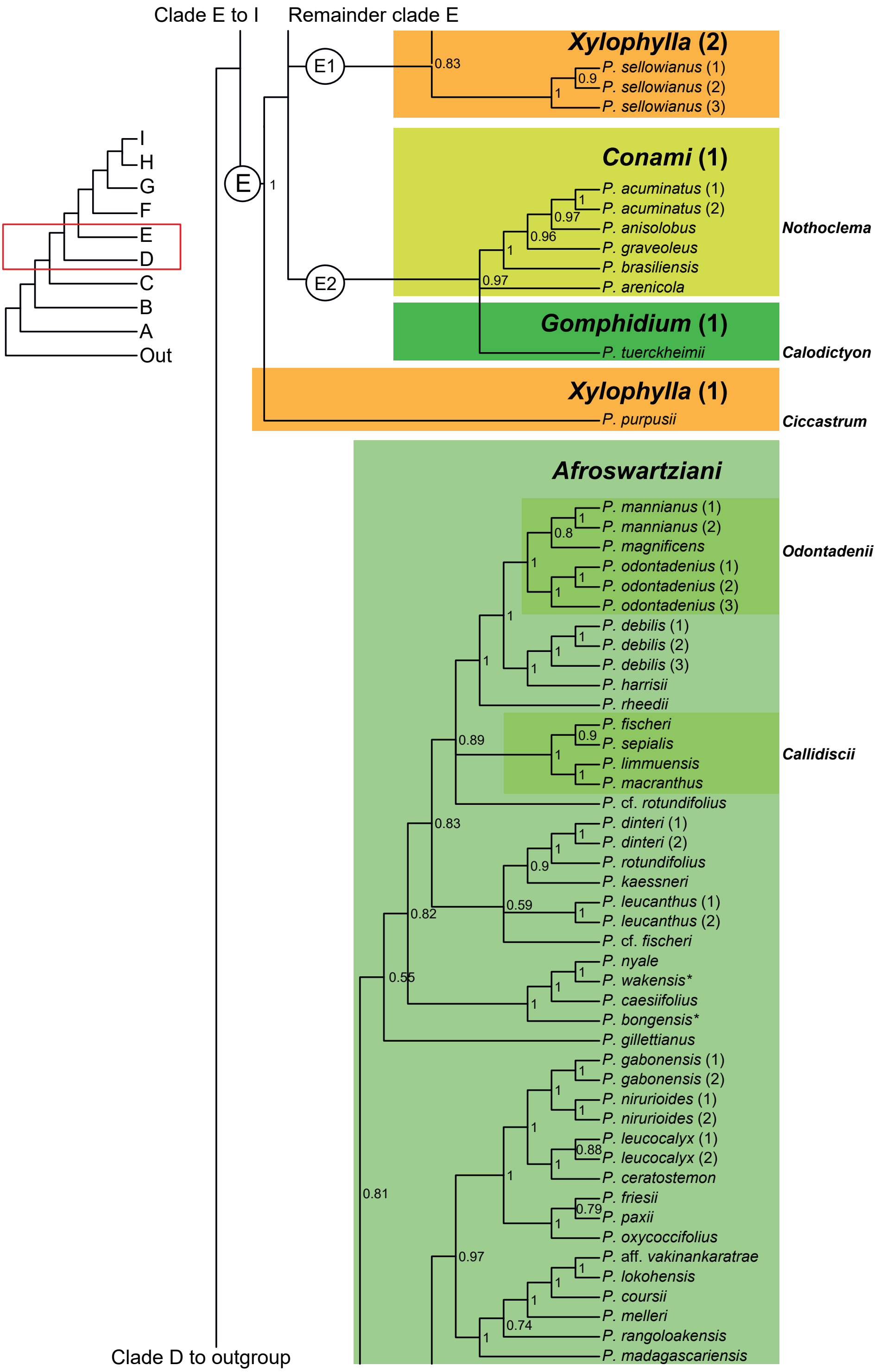


Figure 7-4. Continuation.


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

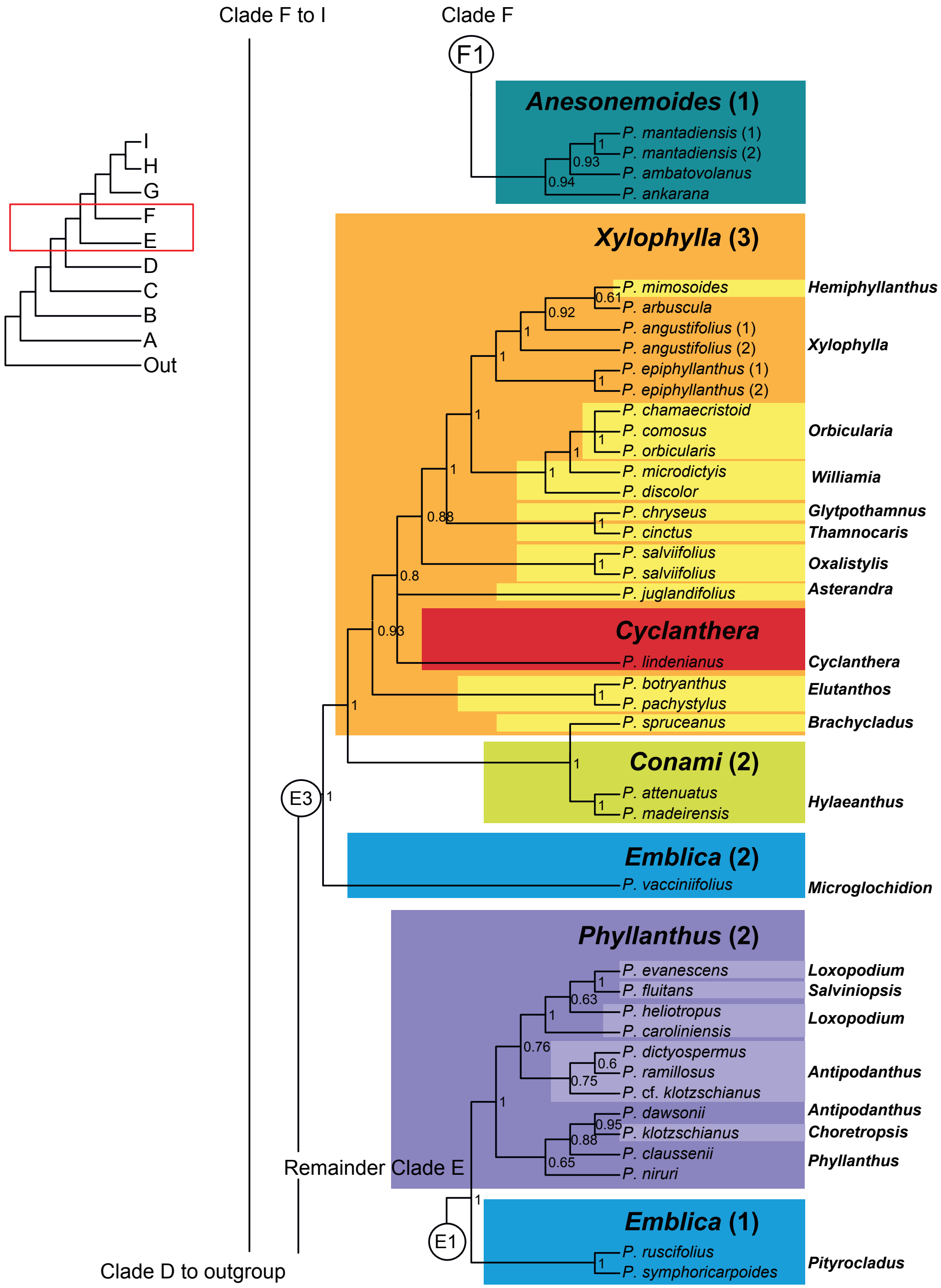
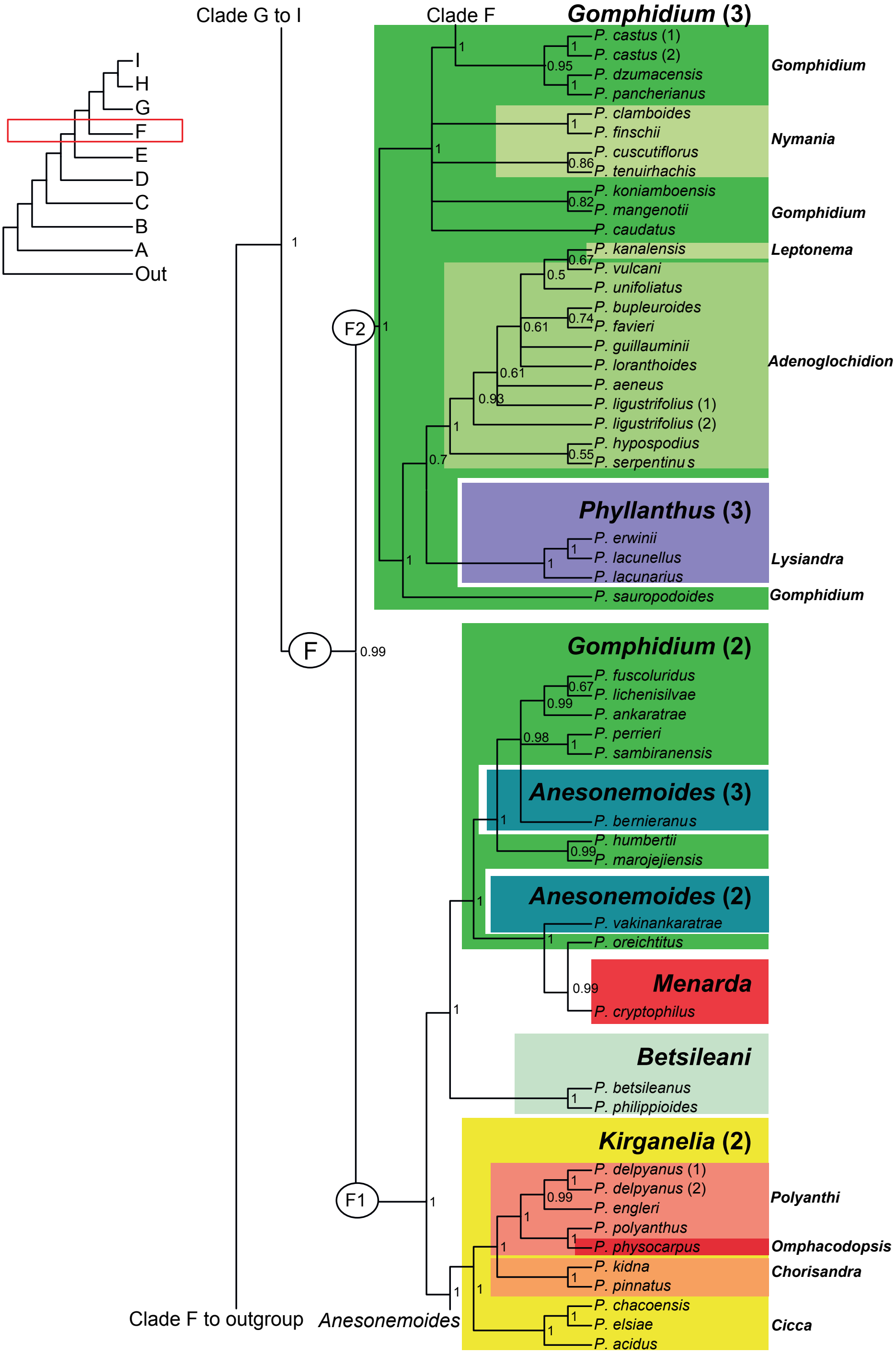


Figure 7-4. Continuation.


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

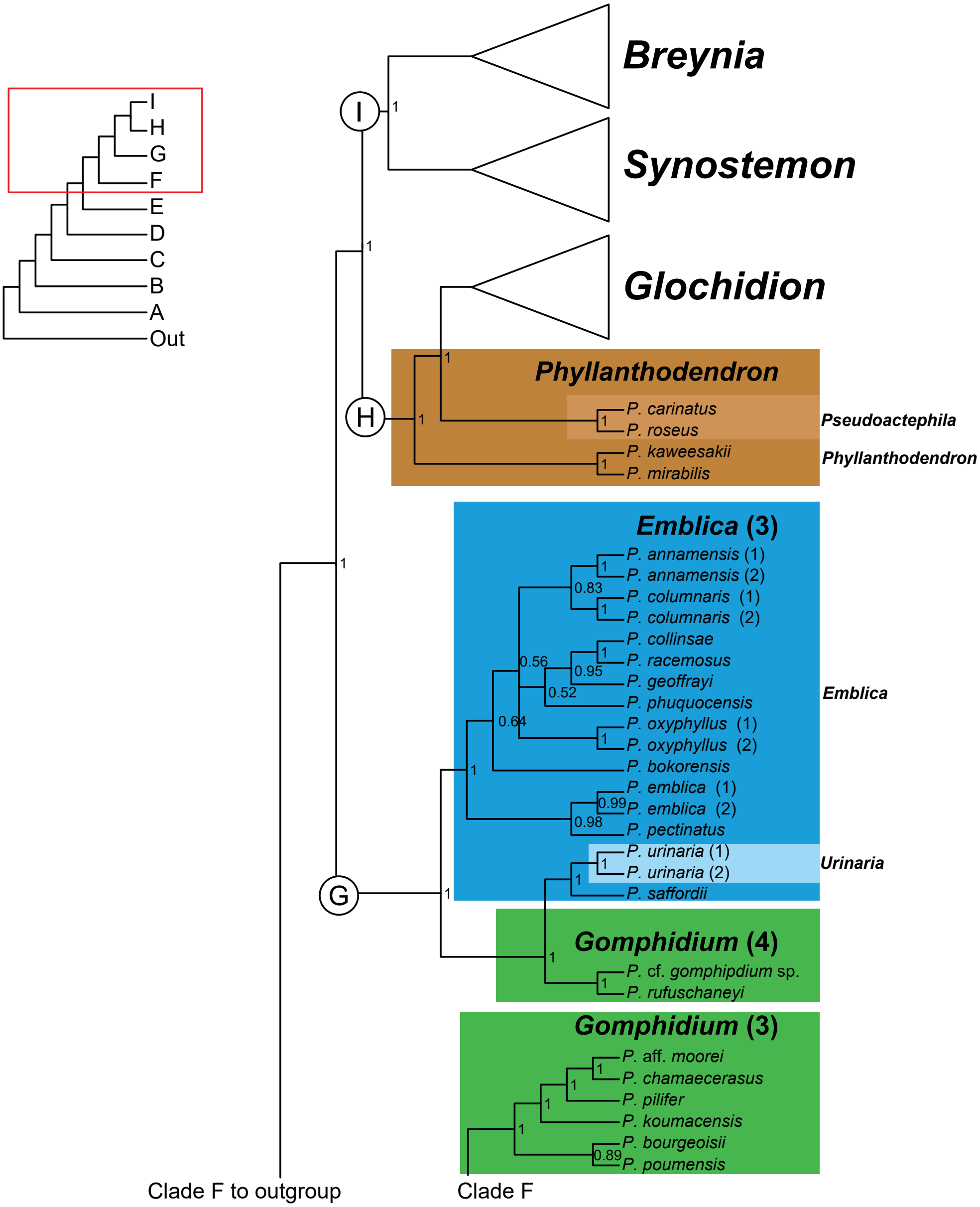


Figure 7-4. Continuation.

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

Non-monophyletic taxa and the subgeneric classification of Phyllanthus

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

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

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

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

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

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

Morphological character evolution

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

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

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

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

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

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

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

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

Conclusion

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

Acknowledgments

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

tax12424-sup-0001-AppendixS1.nex

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

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

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

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

CHAPTER 8

A revised phylogenetic classification of tribe Phyllantheae (Phyllanthaceae)

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Published in Phytotaxa 540: 1-100. 2022

https://doi.org/10.11646/phytotaxa.540.1.1

Chapter 8

A revised phylogenetic classification of tribe Phyllantheae (Phyllanthaceae)

Short title: Revised phylogenetic classification of tribe Phyllantheae

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Abstract

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

Keywords: monophyly; paraphyly; Phyllanthaceae; *Phyllanthus*; systematics

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.* 2014a). Some name changes for this decision have already been implemented for local floras (e.g., Chakrabarty & Balakrishnan 2009b; 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.* 2014a; 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.* 2014a). Unfortunately, this still leaves the remainder of the genus *Phyllanthus* as a paraphyletic group, badly in need of resolution.

The genus *Phyllanthus* as currently circumscribed contains almost 900 species (Bouman *et al.* 2018b), and displays an enormous diversity both in vegetative and floral characters (Webster 1956). Some species were originally placed in separate genera due to their morphological distinctiveness (see Baillon 1858), but were combined in a broad definition of *Phyllanthus* by Müller (1863, 1866). The extensive morphological diversity within *Phyllanthus* was reflected in numerous sections (Müller 1866), which were usually former genera. These sections were subsequently grouped into subgenera (Webster 1956, 1957, 1958), but new insights from palynological (Punt 1967, 1972, 1980, 1986, 1987; Meewis & Punt 1983; Lobreau-Callen *et al.* 1988; Webster & Carpenter 2002, 2008) and phylogenetic research (Kathriarachchi *et al.* 2006; Pruesapan *et al.* 2008, 2012; Falcón *et al.* 2020; Bouman *et al.* 2021) resulted in many changes to this classification. A large number of species transfers were not implemented and there were no lists of the species in each group. Bouman *et al.* (2018) compiled a list that shows the placements of almost all *Phyllanthus* species based on previous morphological, phylogenetic and taxonomic work. The paper aimed to correct some common misconceptions and provide a workable system for the rest of *Phyllanthus*. Still some remaining issues were discussed in the paper and these require taxonomic and nomenclatural changes (e.g., previously paraphyletic sections and possibly polyphyletic subgenera). Nevertheless, the various subgenera and sections are based on genera formerly recognized as separate from *Phyllanthus* (e.g., *Cicca* in Ridley 1924) and these names provide ideal candidates when deciding on new generic boundaries. According to the synopsis of Bouman *et al.* (2018), *Phyllanthus* consisted of 18 subgenera and 70 sections. Several subgenera are similar as they are sister clades (e.g., subgenus *Swartziani* (G.L.Webster 1955: 53) Ralimanana & Hoffmann (2013: 536) and subgenus *Afroswartziani* Ralimanana & Hoffmann 2013: 538), while others are superficially similar due to convergent evolution (e.g., subgenus *Macraea* (Wight 1852: 27) Brunel (1987: 293) and subgenus *Phyllanthus* section *Loxopodium* Webster 1955: 46). Related and morphologically similar subgenera do not warrant separate recognition. This approach will result in fewer new genera than the estimated 20 clades in Kathriarachchi *et al.* (2006).

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

Methods and results

The following new classification is based on Falcón *et al.* (2020) and Bouman *et*

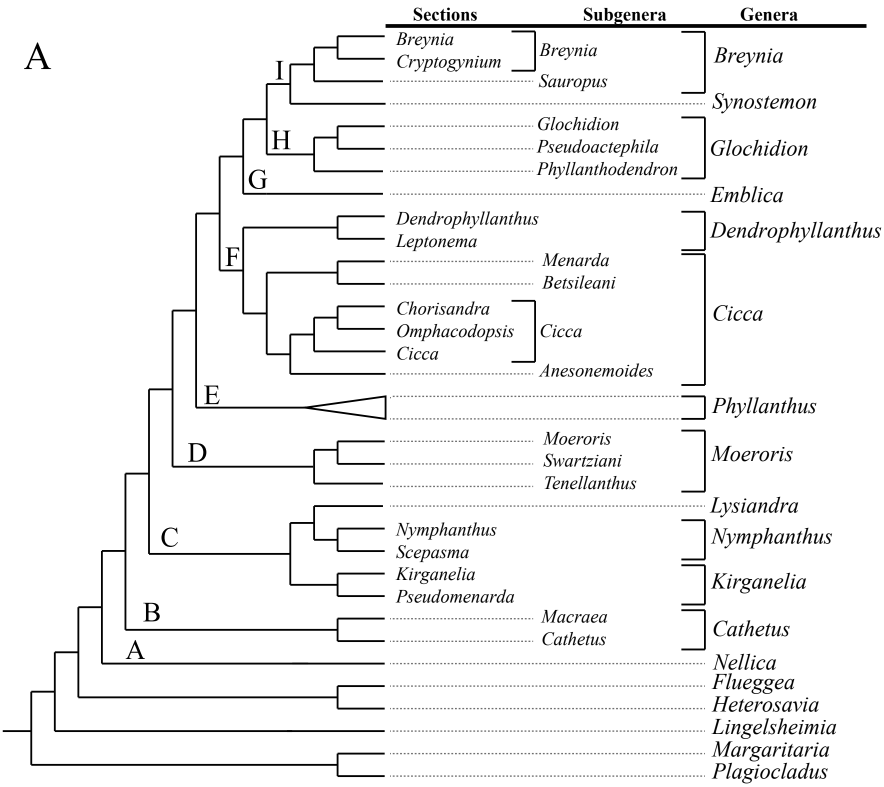


Figure 8-1. (**A**) Summary phylogeny showing relations between genera in tribe Phyllantheae from Bayesian and Maximum Likelihood analysis of five markers (ITS, *PHYC, accD–psaI*, *trnS–trnG, matK*), modified from Supplementary figure 8-1. Classification is shown of genera (right column), subgenera (middle column) and sections (except for the genus *Phyllanthus*. Sections not included in phylogenetic analyses and those for the genus *Flueggea* were omitted.

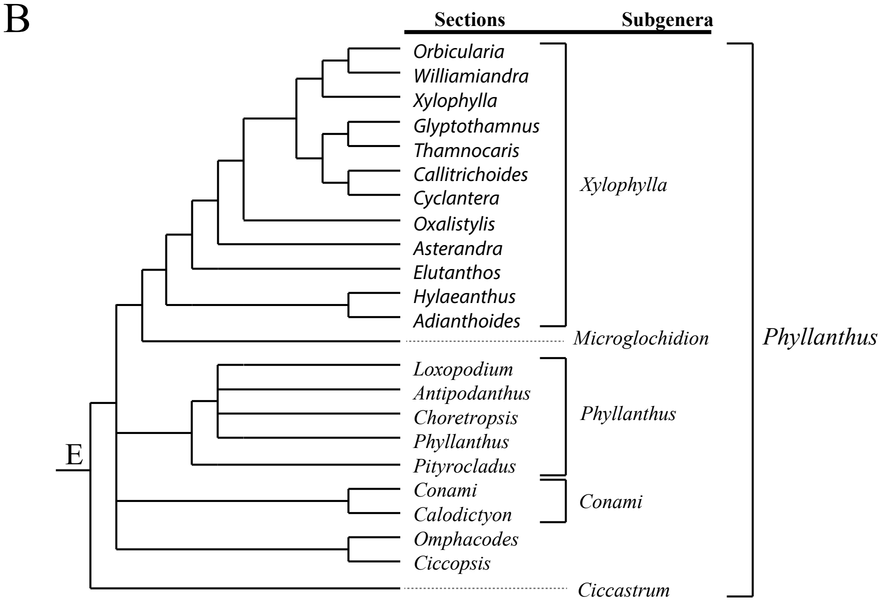


Figure 7-4. Continuation. (**B**) summary phylogeny of the genus *Phyllanthus* as envisioned here with subgenera and sections of groups included in phylogenetic studies shown.

al. (2021) and a new phylogenetic analysis using the data from both studies. This combinend dataset comprises two nuclear DNA regions (the Internal Transcribed Spacers region referred to as ITS, including 5.8S, and the low copy *PHYC*) and three plastid regions (*accD-psaI*, *trnS-trnG* intergenic spacers, and *matK* with portions of the flanking *trnK* intron). GenBank accession numbers are given in Appendix 8-2. 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. 8-1. 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 8-1. The latest phylogeny of *Phyllanthus* and its related genera (the basis for figure 8-1) is presented in Supplementary Figure 1 with the voucher data summarized in Appendix 8-2. 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

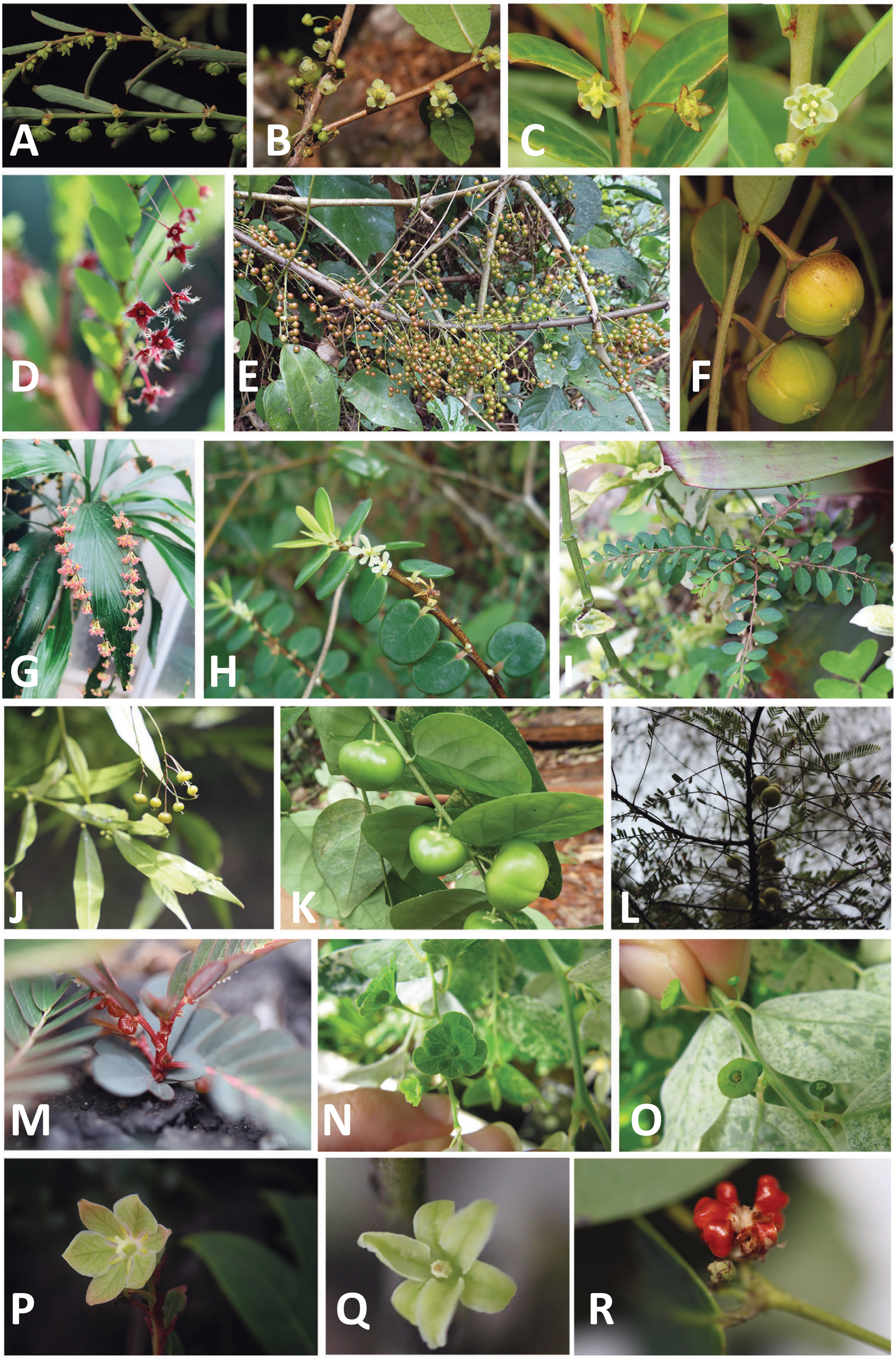
The following is the implementation of a new classification for *Phyllanthus* s.l. including *Breynia*, *Glochidion* and *Synostemon*. The application of the Shenzhen Code (Turland *et al.* 2018) results in name changes to several autonymic sections following article 22.1, such as *Kirganelia* section *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 8-1. 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 8-2.

1. Key to the genera of tribe Phyllantheae

Table 8-1. List of genera in tribe Phyllantheae with global distribution and (estimated) number of species for each group.

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

Nellica Raf.	Africa, Central and North America	20
Nymphanthus Lour.	Australia, mainland Asia, Malesia	86
Phyllanthus L.	Americas, West Indies (some tropical invasives)	213
Plagiocladus Jean F.Brunel	Tropical Africa (Gabon)	1
Synostemon F.Muell.	Australia, mainland Asia, Malesia	41


A
B
C
D
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P
Q
R

Figure 8-2. Images of representative members of tribe Phyllantheae. (A) Flowers of *Nellica maderaspatensis*. (B) Pistillate flowers of *Cathetus gracilis*, note the unique disc covering the ovary. (C) Pistillate and staminate flowers of *Cathetus glaucophyllus*. (D) Staminate flowers of *Nymphanthus glaucescens*. (E) Fruits of *Kirganelia muelleriana*. (F) Fruits of *Lysiandra subcrenulata*. (G) Phylloclade with flowers of *Phyllanthus angustifolius*. (H) Flowering branchlet of *Phyllanthus incrustatus*, note the ornamentation on the axes. (I) Habit of *Moeroris tenella*. (J) Fruiting branch of *Dendrophyllanthus tenuirhachis*. (K) Fruits of *Cicca profusa*. (L) Fruiting branch of *Emblica officinalis*. (M) Flowering plant of *Emblica urinaria*. (N) Pistillate flower of *Breynia disticha*. (O) Staminate flower of *Breynia disticha*. (P) flower of *Glochidion dunnianum*. (Q) Staminate of *Glochidion lanceolarium*. (R) Dehisced capsule of *Glochidion* sp. showing seeds covered with a red sarcotesta. Photos: A & F by J.J. Bruhl; B & P by M.S. Nuraliev; C by T. Williams; E & K by C. Jongkind; H by B. Falcón; J by R.-Y. Yu; D, G, I, L, M, N, O, Q & R by R.W.Bouman.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

14*. Sepals 6 in both sexes; staminate disc urceolate; stamens 3, filaments connate — Asia .... *Cathetus*

14*. Sepals 6 in both sexes; staminate disc not urceolate; stamens 2, filaments free — Africa .... *Plagiocladus*

14*. Sepals 4 in staminate flowers, 6 in pistillate flowers; staminate disc H-shaped around filaments; stamens 2, filaments free — North America .... *Moeroris* (*M. arenaria*)

15. Sepals 5; stamens 5, filaments free — Africa .... *Kirganelia* subgenus *Kirganelia* section *Pseudomenarda*

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

16. Plagiotropic branchlets caducous, usually fascicled (non-phyllanthoid in section *Elutanthos*, but then with paniculate inflorescences); fruits capsules or berries .... *Phyllanthus*

16. Plagiotropic branchlets persistent; inflorescences axillary fascicles, never paniculate; fruits capsules 17

17. Leaves on all axes spirally arranged; filaments connate; pistillate disc consisting of free glands — (North America, Africa and Asia/Australia) .... *Nellica*

17. Leaves on all axes distichous (except at basal nodes in *Cicca*); filaments free or connate; pistillate disc mostly entire (when segmented then filaments mostly free and leaves always distichous) 18

18*. Leaves distichous; pollen 4-colporate; seeds smooth or verrucate — Americas .... *Phyllanthus* subgenus *Phyllanthus* section *Loxopodium*

18*. Leaves distichous; pollen clypeate; seeds smooth or verrucate — Africa, Asia, Australia and Pacific .... *Cathetus* subgenus *Macraea*

18*. Leaves spiral at basal nodes, distichous at upper nodes; pollen grains perisyncolporate with median pores, colpi bordered by parallel muri; seeds smooth or striate — Madagascar .... *Cicca* subgenus *Betsileani*

19. Herbs or subshrubs (small plants with woody base) 20

19. Shrubs to trees, rarely climbers 25

20. Inflorescences unisexual 21

20. Inflorescences bisexual 24

21. Pistillate inflorescences on proximal position and staminate inflorescences on distal position on plagiotropic branchlets; seeds transversely ribbed — ovary often covered with tubercles — pantropical, but origin Asia .... *Emblica* section *Urinaria*

21. Pistillate inflorescences on distal position and staminate inflorescences on proximal position on plagiotropic branchlets; seeds smooth or longitudinally or transversely striate, but not ribbed 22

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

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

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

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

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

27. Filaments fused in sets, rarely free (*K. glauca* & *K. flexuosa*), stamens 2 (*K.*

flexuosa) or 5, connectives not apiculate; fruits baccate — Africa to Australia .... *Kirganelia*

27. Filaments never in sets, free or connate, stamens 3-20, connectives sometimes apiculate; fruits capsules or baccate (then with 3 connate stamens) 28

28. Plagiotropic branchlets sometimes differentiated in vegetative (with larger leaves) and floriferous (with smaller leaves) branchlets, pinnatiform; stamens 3, filaments connate, anthers dehiscing vertically, connectives apiculate; pistillate disc segmented — Asia & Pacific .... *Glochidion*

28. Plagiotropic branchlets not differentiated and all with leaves of similar size (or unifoliate), sometimes bipinnatiform; stamens 3–20, filaments connate or free, anthers dehiscing horizontally to vertically, connectives apiculate or not; pistillate disc entire 29

29. Branchlets (bi-)pinnatiform; sepals often biseriate (inner whorl much longer); staminate disc often of 3 massive emarginate (or 5 separate) segments to absent, stamens may be inserted on a wide receptaculum; stamens usually 3 or 5 (up to 20 in Pacific species); stigmas mostly entire, rarely bifid — pollen 3–(syn-)colporate 30

29. Branchlets pinnatiform; sepal whorls indistinct; staminate disc segmented or entire; stamens 2–7(–15 in species of South America and West Indies) stigmas usually bifid or lacerate 31

30. Inflorescences fascicles or panicles; sepals 5 or 6, filaments free or connate, anthers dehiscing vertically to obliquely, connectives usually apiculate; pollen 3- or 4-syncolporate, exine rugulose-reticulate, vermiculate, pilate or ± vermiculate — Calyx in fruit sometimes saccate — Malesia, Australia, Pacific .... *Dendrophyllanthus*

30. Inflorescences fascicles; sepals 6 (5 in *P. tuerckheimii*), filaments connate (free in *P. tuerckheimii*), anthers dehiscing horizontally (vertically in in *P. tuerckheimii*), connectives rarely elongated; pollen diverse, often 3-colporate or porate with diorate colpi (see Webster & Carpenter 2002), exine vermiculate to pilate — Fruits conspicuously veined — South and Central America .... *Phyllanthus* subgenus *Conami* section *Conami*

31*. Branchlets never transformed to phylloclades; sepals 6; staminate disc segmented; stamens 3, filaments connate, anthers dehiscing vertically, connectives often apiculate; fruits capsules (drupe in *E. officinalis*) — Asia .... *Emblica*

31*. Branchlets never transformed to phylloclades; sepals 5 or 6; staminate disc segmented; stamens 3, filaments connate, anthers dehiscing mostly horizontally to obliquely, connectives rarely apiculate; fruits capsules — mainly Africa .... *Moeroris*

31*. Branchlets sometimes transformed to phylloclades; sepals 4–8; staminate disc mostly segmented, sometimes entire; stamens 3–15, filaments free or fused, sometimes fused in several whorls, anthers dehiscing horizontally to vertically, connectives sometimes apiculate; fruits capsules or berries — Americas.......... *Phyllanthus*

2. Keys to the genera based on geographical distribution

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

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

Africa

1. Branching non-phyllanthoid (laminate leaves and flowers on all axes; branchlets not deciduous).......... 2

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

2. Stamens > 10.......... *Lingelsheimia*

2. Stamens 2–7.......... 3

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

3. Pistillode absent in staminate flowers 4

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

4. Leaves on all axes distichous.......... 6

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

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

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

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

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

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

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

Asia (India to Southeast Asia), Australia and Pacific

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

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

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

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

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

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

7. Disc absent 8
7. Disc present 11

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

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

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

longer than wide; seeds sculptured .... *Synostemon*

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

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

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

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

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

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

staminate disc of 5 or 6 glands; stamens 3 or 4, filaments connate; stigmas mostly bifid; fruits (inflated) capsules (except in *Emblica officinalis*, there spherical drupe 2–3 cm in diam.) 17

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

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

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

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

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

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

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

5. Leaves on all axes spirally arranged; sepals 4 in staminate flowers, 6 in pistillate flowers; staminate disc entire, H-shaped around filaments; stamens 2, filaments free ....*Moeroris* (*M. arenaria*)

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

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

7. Inflorescences unisexual 8
7. Inflorescences bisexual 11

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

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

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

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

12. Inflorescences axillary fascicles on specialized leafless branchlets or cauliflorous; staminate disc absent; stamens 3 or 4, filaments free (3, filaments connate in *C. pseudocicca*); ovary 2- or 3-locular; fruits baccate; seeds without sarcotesta…. .... *Cicca*
12. Inflorescences axillary fascicles, sometimes paniculate; staminate disc

present; stamens 2–15, filaments free or connate; ovary 3–6-locular; fruits baccate (inflorescences then shortly stalked) or capsules; seeds with or without sarcotesta .... *Phyllanthus*

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

Nellica Raf.

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

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

Phyllanthus Linnaeus subgenus *Isocladus* Webster (1956: 345); (1970: 55); Brunel (1987: 317); Ralimanana & Hoffmannn (2011: 334). — *Phyllanthus* L. section *Paraphyllanthus* Müller (1863: 3); (1866: 355); Bentham (1873: 94); Hooker (1887: 285); Boerlaage (1900: 213); Webster (1956: 345); (1997: 209). — *Phyllanthus* L. section *Isocladus*: Brunel (1987: 318). — Type: *Phyllanthus maderaspatensis* Linnaeus = *Nellica maderaspatensis* (L.) Rafinesque ('*maderaspatana*').

Diagnostic features: Herbs or subshrubs, monoecious, branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* spirally arranged on all axes. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 6; disc glands 6, alternating with sepals; stamens 3, filaments connate, anthers dehiscing longitudinally, vertically, connectives not apiculate, not fused; pollen prolate, 3-colporate, colpi monoporate, exine reticulate; pistillode absent. *Pistillate flowers*: sepals 6; disc glands 6, alternating with sepals; ovary 3-locular; style present; stigmas apicallly bifid. *Fruits* capsules. *Seeds* trigonous, verrucate along longitudinal rows.
Distribution: Mainly Africa, Central and North America (USA and Mexico), with one widespread species occurring in Asia and Australia.
Notes —1. *Phyllanthus maderaspatensis* L. of subgenus *Isocladus* G.L.Webster was found to be sister to all other species of *Phyllanthus* (Kathriarachchi *et al.* 2006), while the other species included in subgenus *Isocladus* were present in other clades (as far as they were included in any analysis) and classified in other subgenera/sections. Subsequently, subgenus *Isocladus* was described as monotypic (Ralimanana & Hoffmann 2011), but the *P. maderaspatensis* clade was found to also include the American species *P. polygonoides* (Bouman *et al.* 2021; supplementary fig. 1) and African *P. mendoncae* Jean F.Brunel. This shows that *Phyllanthus*

subgenus *Isocladus* was not monotypic, but was merely the result of incomplete taxon sampling by Kathriarachchi *et al.* (2006). The species placed by Brunel (1987) and Webster (2001b) in the same section as *P. maderaspatensis* should be retained as one group, which is here split from *Phyllanthus* as the separate genus *Nellica*. Unfortunately, the Mexican species of section *Paraphyllanthus* (sensu Webster 2001b) was not included in any phylogenetic study and should be further investigated. Two species by Radcliffe-Smith (1996b) are also included on account of their general resemblance to *Nel. maderaspatensis* (pistillate disc consisting of free glands in the drawing, and spirally arranged leaves), but they need to be further evaluated.
2. The most important characters here are the spirally arranged leaves, non-phyllanthoid branching, the connate stamens with free connectives and a segmented pistillate disc. No further subgeneric groups are currently defined for this genus, but there may be differences between the neotropical and palaeotropical species.

Included species and taxonomic changes (20 spp.):
Nellica barbarae (Johnston 1986: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus barbarae* M.C.Johnst.
Nellica caraculiensis (Brunel 1987: 320) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caraculiensis* Jean F.Brunel.
Nellica cunenensis (Brunel 1987: 320) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cunenensis* Jean F.Brunel.
Nellica ericoides (Torrey 1859: 193) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ericoides* Torr.
Nellica fraguensis (Johnston 1985: 300) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fraguensis* M.C.Johnst.
Nellica galeottiana (Baillon 1860: 32) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus galeottianus* Baill.
Nellica gypsicola (McVaugh 1961: 194) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gypsicola* McVaugh.
Nellica incurva (Thunberg 1794:) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus incurvus* Thunb.
Nellica karibibensis (Brunel 1987: 323) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus karibibensis* Jean F.Brunel.
Nellica liebmanniana (Müller1866: 366) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus liebmannianus* Müll.Arg.
Nellica maderaspatensis (Linnaeus 1753: 982) Raf. (1838: 92, as '*maderaspatana*'). Basionym: *Phyllanthus 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 (Brandegee 1899: 8) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus peninsularis* Brandegee.

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

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

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

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

Cathetus Lour.

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

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

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

Cathetus Lour. subgenus **Cathetus**

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

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

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

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

Diagnostic features: Shrubs, monoecious or dioecious. *Leaves* distichous or in small whorls. *Inflorescences* axillary, unisexual or (rarely) bisexual fascicles. *Staminate flowers*: sepals 6 (4 in *C. petraeus*); disc glands free (urceolate in *C. gracilis*), same number as and alternating with sepals; stamens 3 (2 in *C. petraeus*), filaments and connectives fused into an androphore; anthers elongate; pollen pantoporate or peribrevicolporate, colpi indistinct, exine macroreticulate. *Pistillate flowers*: sepals 6; disc entire; styles present; stigmas 3 with bifid tips. *Fruits* capsules. *Seeds* trigonous, verrucate with verrucae either random or in longitudinal lines.
Distribution: Africa and mainland Asia, Malesia (Java).
Notes —1. The main difference between subgenus *Cathetus* (formerly *Phyllanthus* subgenus *Ceramanthus*) and subgenus *Macraea* is found in the fusion of the

filaments and connectives. Usually the flowers are larger and have two clear dimorphic sepal whorls in *Cathetus* subgenus *Cathetus*.
2. Three sections were recognized in *Phyllanthus* subgenus *Ceramanthus* with little taxonomic value and they are here all subsumed into subgenus *Cathetus*.
3. Pantoporate pollen also occurs in *Nymphanthus*, but they differ in the shape of the apertures (elliptic in *Cathetus*, circular in *Nymphanthus*; Wu *et al.* 2016).

Included species and taxonomic changes (6 spp.):
Cathetus binhii (Thin 1995: 48) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus binhii* Thin.
Cathetus fasciculata de Loureiro (1790: 608), homotypic synonym: *Phyllanthus cochinchinensis* Spreng. (1826: 21).
Cathetus gracilis (Hasskarl 1844: 240) R.W.Bouman, *comb. nov.* Basionym: *Ceramanthus gracilis* Hassk., non *Phyllanthus gracilis* Roxburgh (1832: 654), heterotypic synonym: *Phyllanthus albidiscus* (Ridl.) Airy Shaw (1969: 26).
Cathetus kerstingii (Brunel 1985: 251) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kerstingii* Jean F.Brunel.
Cathetus petraeus (Chevalier & Beille ex Beille 1908: 58) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus petraeus* A.Chev. & Beille ex Beille.
Cathetus welwitschianus (Müller 1864: 330) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus welwitschianus* Müll.Arg.

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

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

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

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

Included species and taxonomic changes (34 spp.):
Cathetus aoraiensis (Nadeaud 1873: 73) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aoraiensis* Nadeaud.
Cathetus beckleri (Müller 1865b: 74) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Phyllanthus beckleri* Müll.Arg.
Cathetus brevipes (Hooker 1887: 297) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus brevipes* Hook.f.
Cathetus chrysanthus (Baillon 1862b: 238) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chrysanthus* Baill.
Cathetus clarkei (Hooker 1887: 297) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus clarkei* Hook.f.
Cathetus distichus (Hooker & Arnott 1832: 95) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus distichus* Hook. & Arn.
Cathetus dumosus (Robinson 1909: 79) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dumosus* C.B.Rob.
Cathetus everettii (Robinson 1909: 80) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus everettii* C.B.Rob.
Cathetus exilis (Moore 1926: 97) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus exilis* S.Moore.
Cathetus filicaulis (Bentham 1873: 111) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Phyllanthus filicaulis* Benth.
Cathetus gardnerianus (Wight 1852: 27) R.W.Bouman, *comb. nov.* Basionym: *Macraea gardneriana* Wight, synonym: *Phyllanthus gardnerianus* (Wight) Baill. (1858: 628).
Cathetus glaucophyllus (Sonder 1850: 133) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus glaucophyllus* Sond.
Cathetus stylosus (Griffith 1848: 33) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus stylosus Griffith*, synonym *Phyllanthus griffithii* Müller 1863: 27.
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 tenuipes (Robinson 1909: 78) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuipes* C.B.Rob.

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

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

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

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

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

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

Kirganelia A.Juss.

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

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

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

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

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

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

Kirganelia A.Juss. section **Kirganelia**

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

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

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

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

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

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

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

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

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

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

2. Four sections are combined to form section *Kirganelia*. Baillon (1858) created the monotypic section *Anisonemopsis*, which was synonymized by Müller (1866) within section *Kirganelia*. *Phyllanthus* section *Floribundi*, which was upheld by Webster (1957), was disentangled and split into several sections by Brunel (1987). His classification of *Kirganelia* was subsequently altered with the results from the phylogenetic studies by Kathriarachchi *et al.* (2006); changes in Ralimanana & Hoffmann (2011), Falcón *et al.* (20202) and Bouman *et al.* (2021, changes implemented here). According to Webster (2002 manuscript of Phyllanthus subgenus *Kirganelia*) species of *Phyllanthus* sections *Flueggeopsis* and *Floribundi* have caducous pistillate sepals, but this has not been studied in detail. Two sections, *Hemicicca* and *Flueggeopsis*, are also subsumed as they are nested within section *Kirganelia*.

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

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

Included species and taxonomic changes (22 spp.):
Kirganelia angavensis (Leandri 1957: 222) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus angavensis* Leandri.
Kirganelia archboldiana (Airy Shaw & Webster 1971:88) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus archboldianus* Airy Shaw & G.L.Webster.
Kirganelia baccata (Mueller ex Bentham 1873: 102) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baccatus* F.Muell. ex Benth.
Kirganelia castica (Willemet 1796: 55) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus casticum* P.Willemet.
Kirganelia ciccoides (Müller 1863: 13) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ciccoides* Müll.Arg.
Kirganelia dinklagei (Pax 1894: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dinklagei* Pax.
Kirganelia flexuosa (Siebold & Zuccarini 1845: 143) R.W.Bouman, *comb. nov.* Basionym: *Cicca flexuosa* Siebold & Zucc., homotypic synonym: *Phyllanthus flexuosus* (Siebold & Zucc.) Müll.Arg. (1866: 324).
Kirganelia fuscolurida (Müller 1866: 346) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fuscoluridus* Müll.Arg.
Kirganelia glaucina (Miquel 1861: 449) R.W.Bouman, *comb. nov.* Basionym: *Anisonema glaucinum* Miq., homotypic synonym: *Phyllanthus glaucinus* (Miq.) Müll.Arg. (1863: 13).
Kirganelia glauca (Wallich ex Müller 1863: 14) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus glaucus* Wall. ex Müll.Arg.
Kirganelia keyensis (Warburg 1891: 355) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus keyensis* Warb.
Kirganelia matitanensis (Leandri 1938: 196) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus matitanensis* Leandri.
Kirganelia microcarpa (Bentham 1861: 312) Hurusawa & Tanaka (*in* Hara 1966: 179). Basionym: *Cicca microcarpa* Benth., homotypic synonym: *Phyllanthus microcarpus* (Benth.) Müll.Arg. (1863: 51).
Kirganelia muelleriana (Kuntze 1891: 597) R.W.Bouman, *comb. nov.* Basionym: *Diasperus muellerianus* Kuntze, homotypic synonym: *Phyllanthus floribundus*

Müll.Arg. (1863: 14), nom. illeg., non *Phyllanthus floribundus* Kunth (1817: 116); nec *Kirganelia floribunda* (Kunth) Sprengel (1826: 48)), homotypic synonym: *Phyllanthus muellerianus* (Kuntze) Exell (1944: 290).

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

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

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

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

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

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

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

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

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

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

Diagnostic features: Shrubs, monoecious, glabrous, branching non/sub-phyllanthoid. *Brachyblasts* absent. *Cataphylls* absent, leaves subtending branchlets not reduced. *Leaves* spiral, present on all axes. *Staminate flowers*: sepals 5; disc glands 5, free, massive, alternating with sepals; stamens 5, filaments free, anthers dehiscing longitudinally, vertically; pollen 3-(4-)colporate, colpi diploporate, sometimes monoporate, exine microreticulate. *Pistillate flowers*: sepals 5; disc entire in *K. somalensis*, segmented in *K. purpureus*; ovary 3-locular; style present; stigma tips bifid and dilated, reflexed. *Fruits* capsules. *Seeds* trigonous, smooth.
Distribution: Tropical Africa.
Note — Two species from Africa have leaves that subtend the branches and are present on all axes (Brunel 1987); the species in section *Kirganelia* have cataphylls subtending the branchlets, though juvenile plants may at first show laminate leaves

(Bouman, *et al.* 2021, fig. 1).

Included species and taxonomic changes (2 spp.):
Kirganelia purpurea (Müller 1864: 329) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus purpureus* Müll.Arg.
Kirganelia somalensis (Hutchinson *in* Brown et al. 1912: 710) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus somalensis* Hutch.

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

Phyllanthus L. subgenus *Lysiandra* Mueller (1859: 108). — *Phyllanthus* L. section *Lysiandra* (F.Muell.) Webster (1978: 573). — Type: *Phyllanthus subcrenulatus* F.Muell. = *Lysiandra subcrenulata* (F.Muell.) R.W.Bouman.
Phyllanthus L. section *Antipodanthus* auct. non G.L.Webster: Webster (2002b: 290), p.p., only Australian species.

Diagnostic features: Shrubs, monoecious or dioecious, glabrous, branching (sub) phyllanthoid. *Brachyblasts* absent. *Cataphyllary stipules* triangular, membranous, base auriculate. *Cataphylls* if present triangular, leaves on penultimate axes mostly not reduced to scales. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6, alternating with sepals; stamens 3, filaments free or nearly so, connective enlarged, anthers discrete, dehiscing horizontally, connectives non-apiculate; pollen subglobose or spheroidal, 3- or 4-colporate, colpi monoporate, exine tectate-reticulate to tectate-perforate; pistillode absent. *Pistillate flowers*: sepals 5 or 6; disc shallowly cupuliform; ovary 3-locular; style present or absent; stigmas mostly bifid. *Fruits* capsules, subglobose. *Seeds* trigonous, scalariform with minute transverse striations or smooth.
Distribution: Endemic to Australia.
Notes —1. Originally this group was created for some Australian species of *Phyllanthus*. *Lysiandra* was confused with *Phyllanthus* section *Antipodanthus* G.L.Webster (Webster 1978, 2002b), but the recent phylogeny in Bouman *et al.* (2021) showed that the two groups fall in different clades. Section *Antipodanthus* is strictly neotropical and is retained here in the genus *Phyllanthus*, whilst *Lysiandra* is Australian. The group is distinct from section *Antipodanthus* and is placed at the same rank as the genera *Kirganelia* and *Nymphanthus*.
2. *Lysiandra* is difficult to distinguish from *Cathetus* subgenus *Macraea*, with which it has an overlapping distribution in Australia. However, species of *Lysiandra* can be distinguished by stipules with truncate bases and the transverse striations on the seeds (stipule base auriculate and seeds smooth or with longitudinally arranged verrucae in *Cathetus* subgenus *Macraea*). Some species also display phyllanthoid branching, which is never found in subgenus *Macraea*.
3. Webster (1978) placed *P. harrimannii* G.L.Webster in section *Lysiandra* (F.Muell.)

G.L.Webster (his circumscription, different from what is presented here). This species is here treated as part of the neotropical *Phyllanthus* section *Antipodanthus*, which seems geographically more consistent.
4. Two species, *P. occidentalis* Hunter & Bruhl (1997c: 157) and *P. striaticaulis* Hunter & Bruhl (1996: 133) are not listed below to prevent unnecessary combinations as they will be synonymized in an upcoming revision of the genus *Lysiandra* (Telford unpublished manuscript).

Included species and taxonomic changes (25 spp.):
Lysiandra arida (Bentham 1873: 110) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aridus* Benth.
Lysiandra australis (Hooker 1847: 284) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus australis* Hook.f.
Lysiandra baeckeoides (Hunter & Bruhl 1997b: 149) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baeckeoides* J.T.Hunter & J.J.Bruhl.
Lysiandra calycina (Labillardière 1806: 75) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus calycinus* Labill.
Lysiandra carpentariae (Müller 1865b: 72) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carpentariae* Müll.Arg.
Lysiandra cauticola (Hunter & Bruhl 1997b: 151) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cauticola* J.T.Hunter & J.J.Bruhl.
Lysiandra collina (Domin 1927: 320) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus collinus* Domin.
Lysiandra dallachyana (Bentham 1873: 104) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dallachyanus* Benth.
Lysiandra eremica (Barrett & Telford 2015: 152) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus eremicus* R.L.Barrett & I.Telford.
Lysiandra eutaxioides (Moore 1920: 216) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus eutaxioides* S.Moore.
Lysiandra flagellaris (Bentham 1873: 106) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus flagellaris* Benth.
Lysiandra fuernrohrii (Mueller 1855: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fuernrohrii* F.Muell.
Lysiandra gunnii (Hooker 1847: 284) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gunnii* Hook.f.
Lysiandra hamelinii (Telford & Barrett 2015: 155) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hamelinii* I.Telford & R.L.Barrett.
Lysiandra hirtella (Mueller ex Müller 1863: 22) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hirtellus* F.Muell. ex Müll.Arg.
Lysiandra indigoferoides (Bentham 1873: 110) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus indigoferoides* Benth.
Lysiandra involutus (Hunter & Bruhl 1997c: 155) R.W.Bouman, *comb. nov.*

Basionym: *Phyllanthus involutus* J.T.Hunter & J.J.Bruhl.

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

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

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

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

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

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

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

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

Nymphanthus Lour.

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

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

Distribution: Australia, mainland Asia, Malesia.

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

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

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

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

Nymphanthus Lour. section **Nymphanthus**

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

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

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

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

Phyllanthus L. subgenus *Eriococcus* (Hassk.) Croizat & Metcalf section *Eriococcus* subsection *Spiciferens* Brunel (1987: 231. — Type: *Phyllanthus nhatrangensis* Beille = *Nymphanthus nhatrangensis* (Beille) R.W.Bouman.
Phyllanthus L. subgenus *Cicca* (L.) G.L.Webster section *Discofractus* Thin (1999: 49). — Type: *Phyllanthus discofractus* Croizat (formerly *Phyllanthus gracilipes* (Miq.) Müll.Arg.) = *Nymphanthus gracilis* (Hassk.) R.W.Bouman.
Phyllanthus L. subgenus *Eriococcus* (Hassk.) Croizat & Metcalf section *Eriococcus* subsection *Integra* Thin (1999: 54). — Type: *Phyllanthus rubescens* Beille. = *Nymphanthus rubescens* (Beille) R.W.Bouman.

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual (subtended by scales in *Nym. nhatrangensis*). *Staminate flowers*: sepals 4; disc glands 4, free; stamens 2 or 4, filaments connate; anthers dehiscing horizontally (rarely vertically). *Pistillate flowers*: sepals 5 or 6; disc cupuliform; ovary 3-locular (6-locular in *Nym. ruber*); style absent; stigmas bifid. *Fruits* (inflated) capsules. *Seeds* trigonous, smooth or striate.
Distribution: Mainland Asia, Malesia and Australia.
Notes —1. *Reidia polyphylla* Wight is selected as the lectotype for the genus *Reidia* by Webster in his manuscripts (see Webster 2002 Manuscript synopsis of subgenus *Eriococcus*; typification effectively published here), because among Wight's species it has the characteristic lacerate sepals. Different type species were listed for *Reidia* in Pfeizer (1848: *Reidia tetrandra* (Roxburgh) Narayanswami) and Chakrabarty & Balakrishnan (2018: *Reidia floribunda*), which might be considered as inadvertent lectotypifications.
2. A few sections formerly retained in *Phyllanthus* subgenus *Eriococcus* are here combined with the former *Phyllanthus* section *Nymphanthus*. These are often monotypic groups that are nested within a paraphyletic section *Eriococcus*. They are combined, but can be resurrected if a full revision of the genus shows the clades to be morphologically distinct. The validity of the formerly established sections was questioned by Webster (1956, 1958), who thought that some species might only show unique character changes (autapomorphies). Thin (1999) divided *Phyllanthus* section *Eriococcus* into two subsections distinguishable based on the sepal margin (entire in *P.* subsection *Integra* Thin and fimbriate in *P.* subsection *Eriococcus*).

Included species and taxonomic changes (78 spp.):
Nymphanthus acutus (Wallich ex Müller 1865b: 75) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus acutus* Wall. ex Müll.Arg.
Nymphanthus armstrongii (Bentham 1873: 112) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus armstrongii* Benth.
Nymphanthus balakrishnanii (Sunil, Kumar & Naveen Kum *in* Sunil *et al.* 2016: 65) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus balakrishnanii* Sunil,

K.M.P.Kumar & Naveen Kum.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Nymphanthus floribundus (Wight 1852: 25, t. 1903) R.W.Bouman, *comb. nov.*

Basionym: *Reidia floribunda* Wight (non *Phyllanthus floribundus* Kunth 1817: 116), homotypic synonym: *Phyllanthus cinereus* Müller (1863: 48).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Basionym: *Phyllanthus leptoclados* Benth.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Nymphanthus polyphyllus (Wight 1852: 28, t. 1904(4)) R.W.Bouman, *comb. nov.* Basionym: *Reidia polyphylla* Wight (non *Phyllanthus polyphyllus* Willdenow

1805: 586), homotypic synonym: *Phyllanthus anabaptizatus* Müller (1866: 421).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Diagnostic features: Shrubs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present or absent. *Leaves* distichous. *Inflorescences* axillary, unisexual, flowers solitary, sessile or subsessile. *Staminate flowers*: sepals 4; disc glands 4; stamens 2, filaments connate, anthers dehiscing horizontally. *Pistillate flowers*: sepals 5, rarely 6; disc entire or 5, rarely 6 free glands; ovary (4- or) 5–8-locular; styles present or absent; stigmas usually entire (bifid in *Nym. watsonii* (Airy Shaw) R.W.Bouman). *Fruits* capsules. *Seeds* trigonous, smooth to transversely striate with small hairs.
Distribution: Malesia (Peninsular Malaysia, Java, Borneo, Philippines, Papua New Guinea) to Australia.
Note — A relatively small section accommodating a few glabrous species from Southeast Asia, mainly recognized by their staminate flowers that appear closed with erect sepals (as opposed to spreading at maturity in the rest of the genus) and

usually entire stigmas. Airy Shaw (1976) discussed at length the mistake by Müller (1866) and Warburg (1894) in interpreting the stamen fusion and anther dehiscence of this section and suggested also that some of the Philippine species might be combined with *Nym. lamprophyllus* (Bouman *et al.* in prep.).

Included species and taxonomic changes (8 spp.):
Nymphanthus anisophyllaeoides (Merrill 1925: 465) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus anisophyllaeoides* Merr.
Nymphanthus balgooyi (Hoffmann & Baker in Hoffmann *et al.* 2003: 195) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus balgooyi* Petra Hoffm. & A.J.M.Baker.
Nymphanthus buxifolius (Blume 1826: 583) R.W.Bouman, *comb. nov.* Basionym: *Scepasma buxifolia* Blume, homotypic synonym: *Phyllanthus buxifolius* (Blume) Müller (1863: 50).
Nymphanthus curranii (Robinson 1909: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus curranii* C.B.Rob.
Nymphanthus lamprophyllus (Müller 1866: 324) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lamprophyllus* Müll.Arg.
Nymphanthus palauensis (Hosokawa 1935: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus palausensis* Hosok.
Nymphanthus robinsonii (Merrill 1912: 405) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus robinsonii* Merr.
Nymphanthus watsonii (Airy Shaw 1971: 493) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus watsonii* Airy Shaw.

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

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

Diagnostic features: Herbs, (sub)shrubs or small trees, monoecious or dioecious, branching (sub-)phyllanthoid (non-phyllanthoid in *M. arenaria* (A.Gray) R.W.Bouman), branchlets pinnatiform (rarely bi-pinnatiform in subgenus *Tenellanthus* (Jean F.Brunel) R.W.Bouman). *Brachyblasts* absent. *Cataphyllary stipules* triangular, usually membranous, subcoriaceous to coriaceous (just as the cataphylls), base unilaterally auriculate. *Cataphylls* triangular, rarely absent and leaves on orthotropic branches not reduced. *Leaves* distichous (or spiral). *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6 (4 in *M. arenaria*); disc glands 5 or 6, free, alternating with sepals (H-shaped in *M. arenaria*); stamens (2)3 or 5(–7 in *M. nummulariifolius* (Müll.Arg.) R.W.Bouman),

filaments free or (partially) connate; anthers globular to elongate, dehiscing obliquely, vertically or horizontally, connectives non-apiculate; pollen usually 3- (or 4-)colporate, colpi monoporate, exine macro- or bireticulate, homobrochate, tectate or microperforate; pistillode absent. *Pistillate flowers*: sepals 5 or 6; disc entire or shallowly cupuliform, sometimes fringed, lobed or divided; ovary 3-locular; style absent or short; stigma tips bifid. *Fruits* capsules. *Seeds* trigonous, smooth, papillose, verrucose or longitudinally striate or banded and transversely striate or barred.
Distribution: Americas, Tropical Africa, Madagascar, few in Asia (few widely invasive species).
Note — Moeroris is the oldest generic name available for this clade, which consists of three main subgenera, *Moeroris* (formerly *Phyllanthus* subgenus *Afroswartziani*), *Swartziani* (G.L.Webster) R.W.Bouman and *Tenellanthus* (Jean F.Brunel) R.W.Bouman. These were originally placed respectively in subgenus *Phyllanthus* (being low subshrubs to herbs) and *Kirganelia* (based on the presence of five stamens). Their pollen was distinct and later it was shown that these groups were phylogenetically distinct and each was raised to subgeneric level (see Ralimanana & Hoffmann 2011, 2014). These subgenera are mainly distinguished by the either unisexual (subgenus *Moeroris* and *Tenellanthus*) or bisexual (subgenus *Swartziani*) inflorescences. The various herbs and subshrubs in this genus have often been treated with other herbaceous species in subgenus *Phyllanthus* from which they are distinguished by the staminate flower and cataphyllary stipules. Herbaceous species of the genus *Emblica* (e.g., *E. urinaria* (L.) R.W.Bouman) can be distinguished by the same characters, but also by the organization of staminate and pistillate flowers along a branchlet.

Moeroris Raf. subgenus **Moeroris**

Moeroris Raf. subgenus *Moeroris*: Literature and type as under the genus.
Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus* subsection *Pentaphylli* Webster (1955: 54); (1957: 324); (1970: 72).— Type: *Phyllanthus pentaphylla* C.Wright ex Griseb. = *Moeroris pentaphylla* (C.Wright ex Griseb.) Falcón & R.W.Bouman.
Phyllanthus L. subgenus *Phyllanthus* section *Phyllanthus* subsection *Odontadenii* Brunel & Roux (1981: 70); Brunel (1987: 339). — *Phyllanthus* L. subgenus *Afroswartziani* Ralim. & Petra Hoffm. section *Odontadenii* (Jean F.Brunel & Jacq. Roux) Bouman in Bouman *et al.* (2018: 170). —Type: *Phyllanthus odontadenius* Müll.Arg. = *Moeroris odontadenia* (Müll.Arg.) R.W.Bouman.
Phyllanthus L. subgenus *Tenellanthus* Jean F.Brunel section *Tangani* Brunel (1987: 307). — Type: *Phyllanthus kaessneri* Hutch. = *Moeroris kaessneri* (Hutch.) R.W.Bouman.
Phyllanthus L. subgenus *Phyllanthus* section *Anthophyllus* Jean F.Brunel subsection *Callidisci* Brunel (1987: 334). — *Phyllanthus* L. subgenus *Afroswartziani* Ralim.

& Petra Hoffm. section *Callidisci* (Jean F.Brunel) Bouman *in* Bouman *et al.* (2018) 169. —Type: *Phyllanthus callidiscus* Jean F.Brunel (= formerly *Phyllanthus fischeri* Pax) = *Moeroris fischeri* (Pax) R.W.Bouman.

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

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

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

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

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

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

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

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

3. *Phyllanthus* sections *Callidisci* (Jean F.Brunel) R.W.Bouman, *Fluitantoides* Jean F.Brunel, *Microdendron* Jean F.Brunel, *Odontadenii* (Jean F.Brunel & Jacq.Roux) R.W.Bouman and *Praephyllanthus* Jean F.Brunel are here not retained as separate sections, otherwise this would render section *Moeroris* polyphyletic. Subgenus *Moeroris* comprises two clades (see Bouman *et al.* 2021; Supplementary fig. 1), that are both mixed with at least one of the other sections. To prevent polyphyly and because of the lack of morphological distinctness (mainly pollen characters) they are here subsumed. It is possible that some sections might be reinstated after a closer study of the two major clades in subgenus *Moeroris*.
4. Only two species of *Phyllanthus* subsection *Pentaphylli* of Webster (1956, 1958) have been included in a phylogenetic study (Falcón *et. al.* 2020), but as they show a general similarity with the species of genus *Moeroris*, they might prove to be nested within that genus. Further research is needed to test whether the other endemics in Hispaniola and Cuba to conform one or more groups with synapomorphies to define a natural infraclasification inside this subgenus.

Included species and taxonomic changes (179 spp.):
Moeroris airy-shawii (Brunel & Roux 1984: 470) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus airy-shawii* Jean F.Brunel & J.P.Roux.
Moeroris amnicola (Webster 1955: 54) Falcón & R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amnicola* G.L.Webster.
Moeroris ampandrandavae (Leandri 1957: 224) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ampandrandavae* Leandri.
Moeroris andranovatensis (Brunel & Roux 1981: 400) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus andranovatensis* Jean F.Brunel & J.P.Roux.
Moeroris angustata (Hutchinson *in* Fries 1914: 121) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus angustatus* Hutch.
Moeroris ankazobensis (Ralimanana & Hoffmann *in* Ralimanana *et al.* 2013: 542) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ankazobensis* Ralim. & Petra Hoffm.
Moeroris arvensis (Müller 1864: 332) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus arvensis* Müll.Arg.
Moeroris aspersa (Brunel & Roux 1985: 386) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus aspersus* Jean F.Brunel & J.P.Roux.
Moeroris asperulata (Hutchinson 1920: 27) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus asperulatus* Hutch.
Moeroris austroparensis (Radcliffe-Smith 1992: 679) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus austroparensis* Radcl.-Sm.
Moeroris bancilhonae (Brunel & Roux 1980: 175) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bancilhonae* Jean F.Brunel & J.P.Roux.
Moeroris benguelensis (Müller 1864: 331) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus benguelensis* Müll.Arg.

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

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

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

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

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

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

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

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

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

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

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

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

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

Moeroris carunculata (Brunel 1987: 380) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carunculatus* Jean F.Brunel, homotypic synonym: *Phyllanthus pseudocarunculatus* Radcliffe-Smith (1996b: 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 1996b: 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 1996b: 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 (1996b: 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 1996b: 323) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuis* Radcl.-Sm.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Phyllanthus xylorrhizus Thulin.
Moeroris yangambiensis (Brunel 1987: 336) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus yangambiensis* Jean F.Brunel.
Moeroris youngii (Brunel 1987: 335) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus youngii* Jean F.Brunel.
Moeroris zambica (Radcliffe-Smith 1996b: 328) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus zambicus* Radcl.-Sm.
Moeroris zornioides (Radcliffe-Smith 1996b: 328) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus zornioides* Radcl.-Sm.

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

Phyllanthus L. subgenus *Swartziani* (G.L.Webster) Ralimanana & Hoffmann *in* Ralimanana *et al.* (2013: 536). — *Phyllanthus* subgenus *Phyllanthus* section *Phyllanthus* subsection *Swartziani* Webster (1955: 53); (1957: 306); (1970: 68); (2002a: 6); Brunel (1987: 345). — *Phyllanthus* L. section *Anthophyllus* Jean F.Brunel subsection *Swartziani* (G.L.Webster) Brunel (1987: 333). — Type: *Phyllanthus amarus* Schumach. & Thonn. = *Moeroris amara* (Schumach. & Thonn.) R.W.Bouman.
Reverchonia Gray (1880: 107); Pax & Hoffmann (1931: 66); Webster & Miller (1963: 200); Webster (1994: 45). — *Phyllanthus* L. section *Reverchonia* (A.Gray) Webster (2007: 235). —Type: *Reverchonia arenaria* A.Gray (= formerly *Phyllanthus warnockii* G.L.Webster) = *Moeroris arenaria* (A.Gray) R.W.Bouman.

Diagnostic features: Herbs, monoecious, branching phyllanthoid with pinnatiform branchlets or non-phyllanthoid branching (spiral phyllotaxy). *Brachyblasts* absent. *Leaves* distichous or spiral. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals (4)5 or 6; disc glands 5 or 6, free or entire and around base of stamens (H-shaped) in *M. arenaria*; stamens (2 or) 3, filaments entirely or partially connate; anthers dehiscing obliquely or horizontally (vertically in *M. arenaria*); pollen 3-colporate, exine reticulate. *Pistillate flowers*: sepals 6; disc entire; ovary 3-locular, smooth or slightly rugose; style absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or finely striated longitudinally.
Distribution: Africa and North America with some common invasive species.
Note —This group contains an enigmatic species (*M. arenaria*) originially placed in the separate genus *Reverchonia* A.Gray. This species differs in most major characters (staminate flower and branching type) from all others in the subgenus, but retaining it in a separate section, would result in a paraphyletic group.

Included species and taxonomic changes (4 spp.):
Moeroris abnormis (Baillon 1860: 42) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus abnormis* Baill.

Moeroris amara (Schumacher & Thonning 1827: 421) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amarus* Schumach. & Thonn.
Moeroris arenaria (Gray 1880: 107) R.W.Bouman, *comb. nov.* Basionym: *Reverchonia arenaria* A.Gray (non *Phyllanthus arenarius* Beille 1927: 587), homotypic synonym: *Phyllanthus warnockii* Webster (2007: 235).
Moeroris fraterna (Webster 1955: 53) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fraternus* G.L.Webster.

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

Phyllanthus L. subgenus *Tenellanthus* Brunel (1987: 301); Ralimanana & Hoffmann (2011: 358). — Type: *Phyllanthus tenellus* Roxb. = *Moeroris tenella* (Roxb.) R.W.Bouman.
Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Pentandra* Webster (1967b: 333); (1970: 63); (1997: 218); (2001b: 385). — *Phyllanthus* L. subgenus *Tenellanthus* Jean F.Brunel section *Pentandra* (G.L.Webster) Brunel (1987: 313); Schmid (1991: 63). — Type: *Phyllanthus pentandrus* Schumach. & Thonn. = *Moeroris pentandra* (Schumach. & Thonn.) R.W.Bouman.
Phyllanthus L. subgenus *Tenellanthus* Jean F.Brunel section *Loandani* Brunel (1987: 309). — Type: *Phyllanthus loandensis* Welw. = *Moeroris loandensis* (Welw.) R.W.Bouman.

Diagnostic features: Herbs or (sub)shrubs, monoecious, branching (sub) phyllanthoid, branchlets (bi)pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5; stamens (3 in *M. cocumbiensis* (Jean F.Brunel) R.W.Bouman) 5(–7 in *M. nummulariifolius* (Müll.Arg.) R.W.Bouman), filaments free, anthers basifixed, dehiscing longitudinally; pollen subglobose, 3- or 4-colporate, exine reticulate. *Pistillate flowers*: sepals 5, obovate or orbicular; disc entire, shallowly cupuliform; ovary 3-locular, smooth or slightly rugose; style absent or short; stigmas bifid. *Fruits* capsules, style persistent or caducous. *Seeds* trigonous, papillose or verrucose.
Distribution: Mainly Africa with one common invasive (*M. tenellus* (Roxb.) R.W.Bouman).
Notes —1. Previously placed in subgenus *Kirganelia* on the basis of the 5-merous staminate flowers (Webster 1967b), 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 1996b: 309) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus manicaensis* Jean F.Brunel ex Radcl.-Sm.

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

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

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

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

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

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

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

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

Phyllanthus L.

Phyllanthus Linnaeus (1753: 981); de Jussieu (1824: 21); Gaertner (1790: 125); Baillon (1858: 621); Müller (1866: 274); Hooker (1887: 285); Webster (1994: 44); (1997: 206); Radcliffe-Smith (2001: 38); Webster (2014: 78); Chakrabarty

& Balakrishnan (2018: 258). — *Phyllanthus* L. section *Euphyllanthus* Grisebach (1859: 33), nom. inval.; Baillon (1860: 24); (1862b: 237); (1865: 351); Müller (1863: 3); (1866: 374). — Lectotype (designated by Small 1913): *Phyllanthus niruri* L.

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

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

Notes —1. The genus *Phyllanthus* is here drastically reduced in size: it now comprises fewer than 200 species and it is mainly distributed in the Americas. Morphological variation within the genus remains extensive, with some overlap with other genera. This is a direct consequence of widespread morphological convergence in the tribe *Phyllantheae* and is the main cause of many of the taxonomic problems that have plagued this group. There is not a set of characters unique to *Phyllanthus* as there are always some exceptions. Geographically, species

in the genus *Phyllanthus* are restricted mostly to the Americas, aside from some invasive species like *P. niruri*. Genera previously classified in a broader treatment of *Phyllanthus* that are also found in South America are *Moeroris* and a few species of *Cicca*. *Phyllanthus* in its current circumscription can be distinguished from other genera in tribe Phyllantheae mainly by comparing specifically similar sections or subgenera. For example, *Phyllanthus* section *Loxopodium* is very similar to *Cathetus* subgenus *Macraea* and these groups are mainly distinguished by their pollen and some vegetative characters, but they are geographically separated. *Nymphanthus* is easily distinguished from *Phyllanthus* on the basis of its tetramerous flowers; these also occur in *Phyllanthus* section *Glyptothamnus* G.L.Webster, but the staminate flowers in the latter have an entire disc (versus free glands in *Nymphanthus*). Some species of *Phyllanthus* subgenus *Conami* (Aubl.) G.L.Webster or *Microglochidion* Müll.Arg. can resemble those in *Cicca* subgenus *Gomphidium*, differing mainly in their pollen, staminate flowers (filaments fused or not) or pistillate flowers (shape of the styles and stigmas).
2. For some species listed below we could not determine their subgeneric alignment due to the unavailability of specimens, unresolved phylogenetic relationships or incomplete descriptions. Webster in one of his unpublished manuscripts (2002 outline of the Neotropical *Phyllanthus*), discussed the affinity of *P. orinocensis* Steyerm. (Steyermark *et al.* 1952: 321) and *P. bolivarensis* Steyerm. (Steyermark *et al.* 1952: 317) and considered them to be better placed in the genus *Sebastiania* Spreng. (Euphorbiaceae), but this has not yet been confirmed.
3. Section *Ciccopsis* is retained in *Phyllanthus*, but placement in any specifc subgenus awaits further phylogenetic studies to resolve its full affinities. Falcón *et al.* (2020) recovered *P. pseudocicca* Grisebach (1865: 166) in a large Neotropical clade with weak support as close to subgenus *Conami*.

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

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

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

Diagnostic features: Shrubs or trees, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, on separate branchlets; either only proximal

staminate inflorescences subtended by cataphylls and distal bisexual inflorescences associated with normally developing leaves. *Staminate flowers*: sepals 6, reflexed; disc glands 6; stamens 3, filaments free, sometimes fused at base, anthers ovoid, dehiscing horizontally; pollen grains 3-colporate, aperture angular, exine reticulate. *Pistillate flowers:* sepals 6; disc entire, 3-angled; ovary 3-locular; styles absent; stigmas bifid. *Fruits* capsules with fleshy exocarp. *Seeds* trigonous, minutely verrucate along longitudinal lines.
Distribution: West Indies (Cuba).
Note —Webster (1957) did not include a description of the fruits and seeds of this monotypic section and its affinities remain unclear, but recent collections indicate that the fruits are capsular with 6 similar trigonous verrucate seeds (Falcón & Leyva 2020). Webster (1957) discussed the affinities of this species with section *Cicca*, but also with his *Phyllanthus* subgenus *Kirganelia* and possibly *Phyllanthus* subgenus *Xylophylla* section *Omphacodes*. Falcón *et al.* (2020) found it related to other Neotropical species of *Phyllanthus*, but its exact relation to extant subgenera is not resolved (supplementary fig. 1).

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

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

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

Diagnostic features: Trees, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5, free or slightly united; stamens 3 (or 4), filaments connate, anthers muticous, dehiscing obliquely; pollen clypeate, exine shields polybrochate, reticulate. *Pistillate flowers*: sepals 5; disc shallowly cupuliform, tenuous (thin), margin undulate (wavy), not pitted; ovary 3-locular; style absent; stigmas bifid, branches rather thick. *Fruits* massive, indehiscent capsules, outer layer somewhat fleshy. *Seeds* trigonous, pairs often unequal, obscurely striate.
Distribution: West Indies.
Note —Falcón *et al.* (2020) found that *P. subcarnosus* was not a part of *Phyllanthus* subgenus *Xylophylla*, which is also confirmed here (supplementary fig. 1). More information is necessary to resolve its relationship within *Phyllanthus*.

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

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

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

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

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

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

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

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

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

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

(1957: 371). — Type: *Phyllanthus orbiculatus* Rich.

Diagnostic features: Herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphylls* oblong-ellipic, membranous. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 6, whorls indistinct; disc glands 6; stamens 3, filaments free; anthers emarginate, dehiscing horizontally; pollen grains spheroidal, pantoporate, exine pilate. *Pistillate flowers*: sepals 6, one type; disc 6 segments; ovary 3-locular; style short; stigmas appressed to the ovary, bifid to halfway, tips incurved. *Fruits* capsules, veins indistict. *Seeds* trigonous, verrucate.
Distribution: Tropical South America.
Note — A monotypic section that differs significantly in habit and staminate floral morphology from *Phyllanthus* subgenus *Conami* section *Conami*. Webster (1957) placed this species in *Phyllanthus* subgenus *Conami* on the basis of the pilate exine, but this character was shown to have evolved several times (Meewis & Punt 1983; Bouman *et al.* 2021).

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

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

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

Diagnostic features: Shrubs, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphylls* probably present, but not seen or described. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers:* sepals 5, whorls indistinct; disc 3 duplex glands; stamens 3, filaments free; anthers muticous, anther slits longitudinal, dehiscing vertically; pollen 3-colporate or syncolporate, exine coarsely reticulate. *Pistillate flowers*: sepals 5; disc 5-angled, entire; ovary 3-locular; style present; stigma tips bifid. *Fruits* and seeds unknown.
Distribution: Central America: Guatemala and Mexico (Chiapas).
Note — Webster (1967a) described this species and placed it in a new section within *Phyllanthus* subgenus *Gomphidium* (Baill.) G.L.Webster. However, it is sister to subgenus *Conami* section *Conami* (supplementary fig. 1) and is here transferred. Free stamens occur in all subgenera of *Phyllanthus* and could perhaps be plesiomorphic.

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

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

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

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets bipinnatiform. *Brachyblasts* absent. *Cataphylls* triangular, indurate. *Leaves* distichous, laminate leaves present on ultimate and penultimate axes. *Inflorescences* axillary, bisexual fascicles, usually on lateral (ultimate branches), sometimes on main axes. *Staminate flowers*: sepals 6, in two whorls; disc entire to dissected, usually 3 duplex glands; stamens 3, filaments connate, anthers dehiscing horizontally, connective sometimes elongated; pollen 3-colporate, colpi diploporate, or pantoporate with elongated colpi, exine varying from reticulate to vermiculate and pilate. *Pistillate flowers*: sepals 6, in two whorls; disc usually cupular; ovary 3-locular; style absent or short; stigmas erect or spreading, slender or dilated, bifid to lacerate. *Fruits* capsules, conspicuously veined. *Seeds* trigonous, sometimes asymmetric, smooth or puncticulate.
Distribution: Tropical South America and West Indies.
Note — The same nomenclatural issue as in *Kirganelia* is raised here as Webster (1955) created section *Nothoclema* as the type section for subgenus *Conami*. He later rectified this (Webster 1960), but did not follow it accordingly in subsequent papers (e.g., Webster 2003). The autonym name for this section, *Conami*, is applied here.

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

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

Phyllanthus L. subgenus *Microglochidion* (Müll.Arg.) Brunel (1987: 237). — *Glochidion* J.R.Forst. & G.Forst. section *Microglochidion* Müller (1863: 58, 69); Pax & Hoffmann (1931: 58). — *Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz section *Microglochidion* (Müll.Arg.) Müller (1865a: 370); (1866: 322); Jablonski (1967: 89). — Lectotype (designated by Jablonski 1967): *Glochidion vacciniifolium* Müll.Arg. (= *Phyllanthus vacciniifolius* (Müll.Arg.) Müll.Arg.)
Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Francavillani* Brunel (1987: 236). —Type: *Phyllanthus francavillanus* Beille (= *Phyllanthus myrsinites* Kunth subsp. *francavillanus* (Mül.Arg.) G.L.Webster)

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* distichous, often with laminal glands. *Inflorescences* axillary, unisexual fascicles (or flowers (sub) solitary). *Staminate flowers*: sepals 6; disc glands 3 (then opposite to stamens) or 6; stamens 3, filaments completely free or basally connate, anthers elongate, dehiscing extrorse, vertical, connectives apiculate; pollen (sub)prolate to subspheroidal, 4–11- colporate, colpi mono- or triporate, exine semitectate-reticulate. *Pistillate flowers*: sepals 6; disc entire; ovary 3-locular; styles present; stigmas entire or bifid. *Fruits* capsules. *Seeds* trigonous, unknown.

Distribution: Tropical South America.

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

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

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

Included species (23 spp.): *P. aracaensis* Webster ex Secco & de Rosário (2015: 209), *P. carrenoi* Steyermark in Steyermark & Brewer-Carias (1976: 343), *P. chimantae* Jablonski (1967: 100), *P. duidae* Gleason (1931: 382), *P. huberi* Riina & Berry in

Grande *et al.* (2012: 10), *P. jablonskianus* Steyermark & Luteyn (1984: 317), *P. jauaensis* Jablonski (1972: 865), *P. lediformis* Jablonski (1967: 103), *P. longistylus* Jablonski (1967: 100), *P. maguirei* Jablonski (1967: 105), *P. majus* Steyermark in Steyermark *et al.* (1952: 318), *P. minutifolius* Jablonski (1967: 115), *P. myrsinites* Kunth (1817: 111), *P. neblinae* Jablonski (1967: 107), *P. obfalcatus* Lasser & Maguire (1950: 79), *P. paraqueensis* Jablonski (1967: 104), *P. pycnophyllus* Müller (1866: 322), *P. strobilaceus* Jablonski (1967: 96), *P. subapicalis* Jablonski (1967: 101), *P. tepuicola* Steyermark (1975 publ. 1976: 236), *P. vacciniifolius* (Müller 1863: 69) Müller (1866: 322), *P. ventuarii* Jablonski (1967: 104), *P. websterianus* Steyermark (1958: 17).

Phyllanthus L. subgenus **Phyllanthus**

Phyllanthus L. subgenus *Phyllanthus*: Webster (1957: 170); (1970: 64); Brunel (1987: 329). — Type: *Phyllanthus niruri* L.

Niruri Adanson (1763: 356). — Lectotype (selected by Webster 1994): *Phyllanthus niruri* L.

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

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

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

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

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

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

Diagnostic features: Subshrubs or shrubs, mostly dioecious (except *P. dawsonii* Steyerm.), branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* spiral, petiolate. *Inflorescences* axillary, unisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 3, filaments connate (or free in *P. rosmarinifolius*); anthers orbicular, dehiscing vertically to horizontally; pollen 3- or 4-colporate, colpi monoporate, exine coarsely reticulate. *Pistillate flowers*: sepals 6; disc shallowly cupuliform; ovary 3-locular; style absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or verrucate.
Distribution: Tropical South America.
Note —Originally placed within *Phyllanthus* subgenus *Isocladus* by Webster (2002b), but the group was shown to be nested within *Phyllanthus* subgenus *Phyllanthus* (Bouman *et al.* 2021) and is accordingly transferred. Webster (1966, 2002b) confused some species of *Phyllanthus* subgenus *Lysiandra* with *Phyllanthus* subgenus *Antipodanthus*, leading to some confusion in the study by Kathriarachchi *et al.* (2006), who included only one species of *Lysiandra* (then Australian *Phyllanthus* section *Antipodanthus*).

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

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

Phyllanthus L. subgenus *Phyllanthus* section *Choretropsis* Müller. (1863: 4, 52); Müller (1866: 427); Baillon (1865: 359); Pax & Hoffmann (1931: 65); Santiago *et al.* (2006: 138). — Type: *Phyllanthus choretroides* Müll.Arg.
Phyllanthus section *Xylophylla* auct. non (L.) Baill.: Baillon (1858: 623), pro parte, without type.

Diagnostic features: Erect (sub)shrubs, monoecious, branching phyllanthoid or less frequently not distinguishable when all axes terete; main axes terete, subterete,

succompressed or flattened, smooth or striate, glabrous; branched from the base, rarely branches restricted to the upper part of the plant; plagiotropic branchlets often terete or transformed to phylloclades, phylloclades cylindrical or flattened. *Brachyblasts* absent. *Cataphyllary stipules* triangular, base indurate, auriculate. *Cataphylls* squamiform. *Leaves* reduced to scales on plagiotropic branchlets, similar to the cataphylls. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 2 or 3, rarely 4, filaments free or connate, anthers, dehiscing longitudinally, horizontally or rarely obliquely; pollen 3-5-colporate, exine reticulate. *Pistillate flowers*: sepals 5 or 6; disc shallowly cupuliform; ovary 3-locular, depressed-globose; style present or absent; stigmas bifid to multifid. *Fruits* capsules. *Seeds* trigonous, verrucose or finely reticulate.
Distribution: Tropical South America.
Note —This South American section was often treated together with the West Indian *Phyllanthus* section *Xylophylla* (see Baillon 1865) on account of the reduced leaves and the presence of phylloclades in both sections. However, on closer examination of the flowers, architecture and pollen of the South American species, they were found to differ considerably and Webster (1957) already recommended to separate the South American species to *Phyllanthus* section *Choretropsis* Müll.Arg., which was later formally done by Santiago (1988). For a more extensive study of the whole section and its subsections, see Santiago *et al.* (2006).

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

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

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid; main axes terete; primary branchlets pinnatiform and modified into flattened phylloclades, sometimes bipinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular. *Cataphylls* ovate or elliptic, apex acute. *Leaves* reduced or not. *Inflorescences* axillary, usually bisexual, sometimes unisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 3, rarely 4, filaments free or connate, anthers globose, dehiscing longitudinally, horizontally or rarely obliquely. *Pistillate flowers*: sepals 5 or 6; disc entire; ovary 3-locular; stigmas thick, thin or filiform, rarely flattened, bifid or multifid. *Fruits* capsules, depressed globose or trigonous. *Seeds* trigonous, verrucose or finely reticulate.
Distribution: Tropical South America.
Note —One new name is proposed here for *P. scoparius* Müller (1873:74), because the epithet is illegitimate due to the synonimized name *P. scoparius* Welwitsch (1859: 591). We propose the name *P. saxatilis* Strijk & R.W.Bouman due to the plant occurring mostly on rocky soils (Santiago et al. 2006).

Included species (8 spp.): *P. angustissimus* Müller (1863: 55), *P. dracaenoides* Orlandini & Cordeiro (in Orlandini *et al.* 2021: 1011), *P. edmundoi* Santiago (1988: 46), *P. flagelliformis* Müller (1863: 54), *P. gladiatus* Müller (1863: 52), *P. klotzschianus* Müller (1863: 53), *P. pedicellatus* Orlandini, Cordeiro & Souza (2020: 168).
Phyllanthus saxatilis Strijk & R.W.Bouman nom. nov., homotypic synonym: *Phyllanthus scoparius* Müller (1873: 74), nom. illeg., non *P. scoparius* Welwitsch (1859: 591).

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

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

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid; main axis terete or subterete; plagiotropic branchlets terete, cylindrical, clustered at the upper part of the stem or appearing like a much branched shrub with branchlets originated from the base. *Brachyblasts* absent. *Cataphyllary stipules* straight and broadly triangular, entire, apex acuminate or attenuate. *Cataphylls* narrowly triangular, apex acute or acuminate. *Leaves* alternate. *Inflorescences* axillary, unisexual fascicles. *Staminate flowers:* sepals 5 or 6; disc glands 5 or 6; stamens 2 or 3, filaments connate; anthers dehiscing longitudinally (vertically), rarely horizontally. *Pistillate flowers:* sepals 5; disc entire; ovary 3-locular; styles terete, filiform, erect or horizontal, bifid at the upper part. *Fruits* capsules, depressed globose. *Seeds* trigonous, verrucate or finely reticulate.
Distribution: Tropical South America.
Note — Santiago *et al.* (2006) proposed as name of the subsection *Choretroides*, but according to article 22.1 of the ICN (Turland *et al.* 2018), names of subgeneric groups with the type species included are named as autonym without an author cited.

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

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

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

Synexemia Rafinesque (1825: 2); (1838: 92). — Lectotype (designated here): *Phyllanthus caroliniensis* Walter (formerly *Synexemia caroliniana* Raf.)
Geminaria Rafinesque (1821: 42); (1824: 14). — Type: *Geminaria obovata* Raf. (= *PhylIanthus caroliniensis* Walter).
Phyllanthus L. subgenus *Phyllanthus* section *Salviniopsis* Holm-Nielsen (1979: 279, nom. nud.) ex Brunel (1987: 385). — Type: *Phyllanthus fluitans* Benth. ex Müll. Arg.

Diagnostic features: Annual or perennial herbs or aquatic and *Salvinia*-like, monoecious or dioecious, branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* distichous (blades inflated in *P. fluitans*). *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 3, filaments free, rarely connate at base; anthers subglobose or flattened, dehiscing horizontally; pollen prolate, 3- or 4-colporate, exine with obscure reticulation. *Pistillate flowers*: sepals 5 or 6; disc cupuliform, lobed or appearing as segments from central ring (*P. hyssopifolioides*); ovary 3-locular; style absent or short; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or verrucate.
Distribution: Americas.

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

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

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

Diagnostic features: Herbs or shrubs, monoecious, branching (sub-)phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular to elongate, usually membranous, sometimes indurate and blackened, base auriculate. *Cataphylls* linear, sometimes leaves not reduced to cataphylls in some species (subsection *Clausseniani*). *Leaves* distichous or subopposite. *Inflorescences* axillary, often unisexual fascicles (spiciform thyrses or racemes at end of branchlets in *P. almadensis*). *Staminate flowers*: sepals (4 or) 5 or 6; disc glandular; stamens (2 or) 3 (or 4), filaments free to completely connate, anther thecae usually not completely separate, sometimes deeply emarginate (appearing stipitate), dehiscing vertically to horizontally; pollen mostly subprolate to prolate, 3- or 4-colporate, exine variously

reticulate or tectate-punctate (rarely coarsely reticulate). *Pistillate flowers*: sepals 5 or 6; disc entire or lobed, shallowly cupuliform; ovary 3-locular, glabrous or pubescent; style usuallly absent; stigmas bifid (sometimes only apically emarginate). *Fruits* capsules. *Seeds* trigonous, striate, finely ribbed or verrucate (subsection *Phyllanthus*).
Distribution: Tropical South and Central America, with a pantropical invasive (*P. niruri*).
Note — Herbaceous and small shrubby species of *Phyllanthus* section *Phyllanthus* might prove difficult to distinguish from species of the genus *Moeroris* as they have many similarities in vegetative and floral characters. The subsections of *Phyllanthus* subgenus *Phyllanthus* should be closely compared to species of the genus *Moeroris* to find more distinguishable characters, especially with species such as *M. stipulatus* Raf.

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

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

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

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

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

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

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

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

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

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

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

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

Distribution: Tropical South America, West Indies, with one common invasive (*P. niruri*).
Note —Subsection *Niruri* contains the type species of *Phyllanthus*, *P. niruri*, therefore the
name should follow the rules for autonyms and become subsection *Phyllanthus*.

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

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

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

Diagnostic features: (Scandent) shrubs, monoecious (rarely dioecious), branchlets rough (scabridulous) to hirtellous, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* elongate. *Leaves* distichous. *Inflorescences* axillary, pedicellate, unisexual or bisexual fascicles. *Staminate flowers*: sepals 5 (rarely 6); disc glands 5 (rarely 6); stamens 2–5(–7), filaments connate (rarely free), anthers ovoid, dehiscing horizontally or obliquely, connectives non-apiculate; pollen subprolate, 3- or 5-colporate, colpi monoporate, exine reticulate. *Pistillate flowers*: sepals 5; disc cupular or dissected; ovary 3-locular; style absent; stigmas spreading, bifid to entire. *Fruits* capsules (indehiscent in *P. symphoricarpoides*). *Seeds* trigonous, smooth (puncticulate in longitudinal rows in *P. valerii* Standl.).
Distribution: Tropical South and Central America.
Note —*Phyllanthus* section *Pityrocladus* was originally placed in subgenus *Emblica* based on pollen morphology as both groups have species with usually 4- or 5-colporate pollen. However, section *Pityrocladus* is sister to other species of subgenus *Phyllanthus* and is therefore transferred here. Both sections share some palynological characters, but differ slightly in flower morphology (mostly connate versus free stamens).

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

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

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

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

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

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

Distribution: Tropical South and Central America, West Indies.

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

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

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

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

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Adianthoides* Jablonski ex Brunel (1987: 236). —Type: *Phyllanthus adianthoides* Klotzsch.
Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Brachycladus* Webster (2001b: 384). —Type: *Phyllanthus rupestris* Kunth.

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform, short and fasciculate, with only 5–10 leaves per branchlet. *Brachyblasts* absent, but scale-like remnants of previous branchlets present. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles, staminate flowers grouped, pistillate flowers solitary. *Staminate flowers*: sepals 6; disc entire; stamens 3, filaments free or connate, anthers muticous, dehiscence not described; pollen clypeate, pantoporate, exine shields polybrochate. *Pistillate flowers*: sepals 6; disc entire, shallowly cupuliform; ovary 3-locular; style absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth.
Distribution: Tropical South and Central America.
Notes —1. A group with a complicated taxonomy. Brunel (1987) validated two sections within subgenus *Xylophylla* following recommendations by Jablonski (1967). Jablonski (1967) treated several species together in his "*Adianthoides* group", characterized by their free stamens, large leaves, short globular anthers and bifid styles, and proposed *P. francavillanus* Müller (1863: 20) and *P. adianthoides* Klotzsch as possible types. Jablonksi numbered the species in his treatment and wished to include numbers 20–33, thereby strangely excluding *P. adianthoides* (number 38). *Phyllanthus adianthoides* does not match with its connate stamens (as opposed to free in the others). Even though Brunel (1987) published Jablonski's *Adianthoides* group as two separate sections, the group was found to be heterogenous in other treatments (Webster 1999, 2001b, 2004). *Phyllanthus francavillanus* was reduced to a subspecies of *P. myrsinites* Kunth (Webster 1999) and its section is considered a heterotypic synonym of *Phyllanthus* subgenus *Microglochidion*. Section *Adianthoides*, as circumscribed here, was included by Webster's (2001b) section *Brachycladus* G.L.Webster. The descriptions of both sections overlap greatly (mainly in the entire staminate disc and areolate pollen), but differ in the staminal fusion (strictly free (Brunel 1987) versus free or connate (Webster 2001b)). These two sections should logically be combined as Webster (2001b) already treated all the included species together, but perhaps thought that the group was not officially published yet. Since section *Adianthoides* is the older name, section *Brachycladus* is

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

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

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

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

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

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

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

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

Diagnostic features: Perennial diminutive herbs, monoecious, branching phyllanthoid, main axes from a small rootstock, branchlets pinnatiform and clustered at apex, sometimes rooting at the nodes. *Brachyblasts* absent. *Leaves* distichous, slightly succulent. *Inflorescences* axillary, unisexual fascicles (or flowers solitary). *Staminate flowers*: sepals 5; disc glands 5, purplish; stamens 2, filaments connate; anthers globular, dehiscing horizontally, extrorse, connectives not apiculate; pollen spheroidal, exine with band-shaped shields. *Pistillate flowers*: sepals 6; disc glands 6, free, purplish; ovary 3-locular; style absent; stigma tips bifid or emarginate. *Fruits* capsules, surface rough. *Seeds* trigonous, verrucate.
Distribution: West Indies (Cuba).
Note — Though *P. carnosulus* Müll.Arg. is yet to be included in any phylogenetic study, a species resembling section *Callitrichoides* was found to be nested within subgenus *Xylophylla* (Falcón *et al.* 2020). Webster's (2002) suggestion that the pollen of *Phyllanthus* section *Callitrichoides* can be inferred as stephanocolporate is in line with Brunel's (1987) decision to place this section in subgenus *Microglochidion*. Webster (1957) originally interpreted the pollen as having elongated exine shields, which might prove to be an intermediate between the stephanocolporate pollen of subgenus *Microglochidion* and the clypeate pollen of subgenus *Xylophylla*.

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

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

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

Diagnostic features: Annual or perennial herbs or subshrubs, monoecious, branching phyllanthoid, branchlets pinnatiform (sometimes bipinnatiform). *Brachyblasts* absent. *Cataphyllary stipules* triangular-ovate, membranous, base not auriculate. *Cataphylls* elliptic. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles (or flowers solitary). *Staminate flowers:* sepals 5 or 6; disc glands 5 or 6, free; stamens 2 or 3, filaments connate, anthers completely connate into a disciform circumsessile synandrium, connectives fused and not apiculate; pollen spheroidal, pantoporate, exine honey-comb like clypeate, shields roundish with a single central pilum. *Pistillate flowers:* sepals 6; disc glands 6, free, often purplish; ovary 3-locular; style present or absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous verrucate.
Distribution: West Indies (Cuba, Dominican Republic, Haiti).
Notes —1. *Phyllanthus* subgenus *Cyclanthera* was found to be nested within

Phyllanthus subgenus *Xylophylla* (Falcón *et al.* 2020; Bouman *et al.* 2020). This group of species was originally treated as a section within subgenus *Phyllanthus* and later transferred to *Phyllanthus* subgenus *Xylophylla* (Brunel 1987), before gaining its own subgeneric status (Webster 2002b). The easiest solution seems to be to revert back to Brunel's (1987) decision to retain section *Cyclanthera* within *Phyllanthus* subgenus *Xylophylla*.
2. Webster & Carpenter (2002) provided several theories to explain the origin of the unique pollen morphology of *P. lindenianus* Baill. Affinities to *Phyllanthus* subgenus *Conami* and *Xylophylla* were discussed and section *Cyclanthera* was shown to be nested within the latter group. A close relationship between *Phyllanthus* subgenus *Conami* section *Apolepsis* was also discussed, but this species has yet to be included in a phylogenetic study. However, the absence of muri in the pollen of section *Apolepsis* (Webster & Carpenter 2002) argues against a close relationship, since this would indicate an even more drastic reduction of the clypeate pollen in *Phyllanthus* subgenus *Xylophylla*.

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

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

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

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

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

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

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

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

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

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

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

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Epistylium* (Sw.) Grisebach (1859: 33); Müller (1863: 3, 46); (1866: 412); Pax & Hoffmann (1931: 65); Webster (1958: 153). — *Epistylium* Swartz (1800: 1099); de Jussieu (1824: 17); Baillon (1858: 645). — Lectotype (designated by Webster 1958): *Epistylium axillare* (Sw.) Sw. (= *Phyllanthus axillaris* (Sw.) Müll.Arg.).
Phyllanthus L. section *Catastylium* Grisebach (1859: 33); Müller (1866: 413); Pax & Hoffmann (1931: 64). —Lectotype (designated here): *Phyllanthus cauliflorus* (Sw.) Griseb.

Diagnostic features: Shrubs or (monocaulus) trees, monoecious, glabrous, branching phyllanthoid, branchlets pinnatiform, clustered at the apex of the more or less unbranched stem. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary or cauliflorous thyrses, bisexual fascicles. *Staminate flowers*: sepals 4 or 5; disc glands 4 or 5; stamens 2 or 3, filaments connate; anthers deflexed, dehiscing longitudinally

and obliquely (downward) to horizontally; pollen spheroidal, clypeate, exine reticulate. *Pistillate flowers*: receptacle and calyx massive, sepals 5, erect; disc indistinct, lobed or consisting of 5 glands; ovary subglobose to beaked; style absent; stigmas petaloid, massive, often reflexed at top of ovary or at end of elongated ovarial beak (*P. cauliflorus*). *Fruits* capsules, angled. *Seeds* 1 (by abortion) or 2 per locule, smooth.
Distribution: West Indies.

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

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

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

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

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

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

Phyllanthus L. subgenus *Conami* (Aubl.) G.L.Webster section *Hylaeanthus* Webster (2002b: 293); (2004: 12). — Type: *Phyllanthus attenuatus* Miq.
Meborea Aublet (1775: 825, t 323); Baillon (1858: 656). — Type: *Meborea guianensis* Aubl. (= *Phyllanthus attenuatus* Miq.).

Diagnostic features: Mostly trees, sometimes shrubs, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform (sometimes fascicled on slender permanent stalk), usually subtended by reduced leaves (but generally not reduced to cataphylls), sometimes lenticellate. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual (rarely bisexual) fascicles, sometimes supra-

axillary. *Staminate flowers*: sepals 6 (rarely 5), in two whorls; disc entire and 6-lobed or less often divided into glands; stamens 3, filaments connate (free in *P. skutchii* Standl.); anthers muticous, dehiscing horizontally or obliquely; pollen globose (spheroidal), porate, lacking distinct ectocolpi, exine pilate, heterogenous. *Pistillate flowers*: sepals 6; disc shallowly cupuliform to cupular; ovary 3–6-locular; style present or absent; stigmas bifid to entire. *Fruits* baccate, with fleshy exocarp. *Seeds* smooth, with sarcotesta.
Distribution: Tropical South America.
Note —The apparent relationship between sections *Hylaeanthus* and *Adianthoides* indicated a separate loss of clypeate pollen (discussed in Bouman *et al.* 2021). The difference in pollen morphology is quite surprising as section *Adianthoides* has clypeate pollen with reticulate exine (as is standard for subgenus *Xylophylla*) while pollen of species in section *Hylaeanthus* is simply porate with no colpi and pilate exine (more common in subgenus *Conami*). The differences in pollen morphology are striking and possibly reflect independent origins of the pilate exine within *Phyllanthus*. These groups do show agreement in vegetative characters (see Webster 2002b) and in the morphology of the staminate flower. Both groups have species with usually three stamens and an entire disc.

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

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

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

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

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

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

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

Diagnostic features: Shrubs or small trees, monoecious, branching phyllanthoid (sub-phyllanthoid in *P. formosus*), branchlets pinnatiform. *Brachyblasts* absent. *Inflorescences* axillary, bisexual or unisexual fascicles or with solitary flowers. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6, free or coalescent; stamens 3–7(–15 in *P. discolor* and *P. microdictyus* Urb.), in two whorls, filaments completely or partially connate, can be massive and then whorled on central pillar, anthers dehiscing horizontally or obliquely (sometimes a part of the stamens dehiscing vertically), connectives sometimes apiculate; pollen spheroidal, clypeate, exine shields oligobrochate, reticulate. *Pistillate flowers*: sepals 5 or 6 (or rarely 7 in *P. microdictyus*); disc tenuous to rather massive, sometimes 5-angled (fused with gynophore in *P. microdictyus*); ovary 3-locular, sessile or definitely stipitate (gynophore); style present or absent; stigma tips bifid, often revolute, moderately dilated distally, tips variable from crescent-shaped to lacerate and 4-tipped. *Fruits* oblate capsules, veins conspicuous or obscure. *Seeds* trigonous, verrucate (with longitudinal lines or dark reddish brown dots in *P. discolor*, puncticulate in *P. cristalensis* Urb.).
Distribution: West Indies.
Note —Webster (1958) described three subsections for section *Williamia* (*Discolores*, *Incrustati* and *Mirifici*), that were differentiated based on stem ornamentation and phyllotaxy. *Phyllanthus* subsection *Discolores* contains the type species of section *Williamia* and it is found here to be paraphyletic with species of *Phyllanthus* section *Orbicularia* (Supplementary Fig. 1). Subsection *Discolores* is merged here with section *Orbicularia*. The two other subsections previously placed in Webster's (1958) definition of section *Williamia*, form a monophyletic group (Supplementary Fig. 1) and these are treated here as the reinstated section *Williamiandra* (see below).

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

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

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

Diagnostic features: Shrubs, sometimes arborescent, monoecious, branching

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

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

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

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

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles, flowers appearing with the expanding leaves. *Staminate flowers*: sepals 4 (6, rarely 5 in *P. comptus* G.L.Webster); disc glands 4 (6, rarely 5 in *P. comptus*); stamens 2 (4–8 in *P. comptus*), filaments connate (but free in *P. comptus*), anthers dehiscing vertically; pollen spheroidal, clypeate, exine reticulate. *Pistillate flowers*: sepals 4 (6, rarely 5 in *P. comptus*); disc entire, angled; ovary 3-locular; style absent or present (and elongated); stigmas bifid, tips narrowed to acute. *Fruits* capsules, subglobose. *Seeds* trigonous, smooth or rugulose.
Distribution: West Indies (Cuba).
Note —Differences and similarities with *Nymphanthus acutissimus* were discussed at length by Webster (1955). Vegetatively, these groups can be distinguished by the smaller persistent stipules and thinner leaves in *Nym. acutissimus*. In contrast with section *Thamnocaris*, the inflorescences in *Nym. acutissimus* are unisexual, the pistillate flowers usually have six sepals and the ovary is verrucate.

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

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

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

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets

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

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

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

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

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

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

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

Diagnostic features: Shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform, all axes incrustate with dark platelets of bark, dark or reddish brown to black. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary,

bisexual fascicles. *Staminate flowers*: sepals 5; disc glands 5; stamens (2 or) 3–6, filaments connate in a column, anthers sometimes in 2 whorls (2 sets on top of column), dehiscing longitudinally, vertically and horizontally often in same flower, connectives sometimes apiculate. *Pistillate flowers*: sepals 5–7, unequal; disc entire, massive, sometimes 5-angled; ovary 3-locular; style present or absent; stigmas with conspicuously lacerate endings of 3–6 tips. *Fruits* capsules. *Seeds* trigonous, smooth or with carinate back.
Distribution: West Indies (Cuba).

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

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

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Xylophylla*: Literature and type as under the subgenus.
Genesiphylla L'Héritier de Brutelle (1778: 29); Rafinesque (1838: 92. —*Phyllanthus* L. section *Typhophyllanthus* Kuntze subsection *Genesiphylla* (L'Hér.) Kuntze in Post & Kuntze (1904: 434). — Type: *Genesiphylla asplenifolia* L'Hér., nom. illeg. (= *Xylophylla latifolia* L. = *Phyllanthus epiphyllanthus* L.).
Hexadena Rafinesque (1838: 92). — Type: *Hexadena angustifolia* (Sw.) Raf. (= *Phyllanthus angustifolius* (Sw.) Sw.).
Glochidion J.R.Forst. & G.Forst. section *Hemiphyllanthus* Müller (1863: 59, 71); Pax & Hoffmann (1931: 58). — *Phyllanthus* L. section *Hemiphyllanthus* (Müll. Arg.) Müller (1865a: 370); (1866: 323). — *Phyllanthus* L. subgenus *Xylophylla* (L.) Pers. section *Hemiphyllanthus* (Müll.Arg.) Webster (1955: 62); (1958: 163). — Lectotype (designated by Webster 1955): *Phyllanthus ovatus* Poir.

Diagnostic features: Shrubs or small trees, monoecious, branching phyllanthoid, branchlets (bi)pinnatiform with ultimate axes transformed into broad or thin phylloclades. *Brachyblasts* absent. *Leaves* either reduced to scales or well-developed. *Inflorescences* axillary, unisexual or bisexual fascicles at nodes of phylloclades. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6; stamens 2–6, filaments united at least at the base, anthers dehiscing more or less horizontally; pollen globose, clypeate, exine shields oligobrochate, reticulate. *Pistillate flowers*: sepals 5 or 6; disc segmented to urceolate; ovary 3-locular; style present or absent; stigmas often lobed or bifid, sometimes reduced to short projections from ovary (*P. megapodus* Webster 1955: 62). *Fruits* capsules, oblate, smooth to tuberculate. *Seeds* trigonous or sometimes (when 1 locule developed) ovate and flattened, verrucate (or smooth in *P. maleolens* Urb. & Ekman).
Distribution: West Indies.
Notes —1. The genus *Lomanthes* Raf. was listed as a synonym of section *Xylophylla*

in Webster (1958), but with no re-identification of the type. The type species is listed on The Plant List (2013) as *P. hirtellus* (here *Lysiandra hirtellus*), an Australian endemic, which seems strange considering *Lomanthes* was described from North America. On Index Nominum Genericorum (Farr & Zijlstra 1996), *Lomanthes latifolia* is listed as a synonym of *P. epiphyllanthus*. We have not seen the type material and cannot correctly conclude where this name should be placed.
2. Webster (1956, 1958: 180) selected *Xylophylla latifolia* as the type species for section *Xylophylla* and selected a lectotype for the species. A later typification for section *Xylophylla* with as type *Xylophylla longifolia* (Jarvis *et al.* 1993) as listed in the Index Nominum Genericorum (Farr & Zijlstra 1996) is superfluous.
3. *Phyllanthus* section *Hemiphyllanthus* was found to be nested within a paraphyletic section *Xylophylla* (Bouman *et al.* 2021). Section *Hemiphyllanthus* is very similar to section *Xylophylla* as the branchlets appear like thin phylloclades that still produce laminate leaves. However, there is no trace that the branchlets evolved from an ancestor with bipinnatiform branchlets. Both sections are here combined with as synapomorphy the transformation of branchlets into phylloclades, with or without laminate leaves.

Included species (16 spp.): *P. acacioides* Urban (1902: 287), *P. angustifolius* (Swartz 1788: 28) Swartz (1800: 1111), *P. arbuscula* (Swartz 1788: 28) Gmelin (1791: 204), *P. epiphyllanthus* Linnaeus (1753: 981), *P. eximius* Webster & Proctor in Webster (1960: 283), *P. latifolius* (Linnaues 1771: 221) Swartz (1800: 1109), *P. maleolens* Urban & Ekman in Urban (1928: 60), *P. martii* Müller (1873: 27), *P. megapodus* Webster (1955: 62), *P. mimosoides* Swartz (1788: 27), *P. montanus* (Swartz 1788: 28) Swartz (1800: 1117), *P. myriophyllus* Urban (1921: 36), *P. obtusatus* (Thunberg 1817: 12) Müller (1866: 433), *P. ovatus* Poiret (1804: 297), *P. proctoris* Webster (1958: 195), *P. robustus* Martius ex Colla (1836: 106).

Clade F — Figs. 1, 2J & K (supplementary fig. 1)

Cicca L.

Cicca Linnaeus (1767: 124); de Jussieu (1789: 386); (1824: 20); Baillon (1858: 617); Robinson (1909: 87); Ridley (1924: 216). — *Phyllanthus* L. section *Cicca* (L.) Müller (1863: 3, 50); (1866: 413); Hooker (1887: 287); Boerlage (1900: 213); Pax & Hoffmann (1931: 62). — *Phyllanthus* L. subgenus *Eucicca* Kurz (1873: 238), *nom. inval.* — *Phyllanthus* L. subgenus *Cicca* (L.) Webster (1957: 60); Brunel (1987: 289). — *Phyllanthus* L. subgen. *Kirganelia* (A.Juss.) Kurz section *Cicca* (L.) Webster (2001b: 381). — Type: *Cicca disticha* L. (= formerly synonym of *Phyllanthus acidus* (L.) Skeels) = *Cicca acida* (L.) Merr.
Tricarium de Loureiro (1790: 557). — Type: *Tricarium cochinchinense* Lour. (= formerly synonym of *Phyllanthus acidus* (L.) Skeels = *Cicca acida* (L.) Merr.).

Staurothyrax Griffith (1854: 476). — Type: Not designated (only a *S. spec.* described).

Phyllanthus L. subgenus *Ceramanthus* (Hassk.) Jean F.Brunel section *Ebolowani* Brunel (1987: 412). – Type: *Phyllanthus letouzeyanus* Jean F.Brunel. = *Cicca letouzeyanus* (Jean F.Brunel) R.W.Bouman.

Diagnostic features: Herbs, shrubs or trees, monoecious or dioecious, branching (non-)phyllanthoid, branchlets (bi)pinnatiform (sometimes further ramified), rarely opposite (subgenus *Menarda* (Comm. ex A.Juss.) R.W.Bouman), sometimes specialized in vegetative and floriferous branchlets. *Brachyblasts* present or absent. *Cataphyllary stipules* triangular or spinescent, indurate or membranous, base usually not auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous to opposite, sometimes spiral at base. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 4–6; disc entire or 4–6 glands, sometimes absent; stamens 2–6, filaments mostly free, sometimes (basally) connate, basifixed or connate (in some species of subgenus *Menarda*); anthers dehiscing longitudinally, vertically to obliquely to horizontally, connectives (non-)apiculate; pollen spheroidal or oblate, 3- or 4-(syn)colporate, colpi monoporate (to diploporate in subgenus *Menarda*), exine reticulate (or perforate in subgenus *Menarda*); pistillode absent. *Pistillate flowers*: sepals 4–6; disc entire, segmented or absent; ovary 2–4-locular; styles present or absent; stigmas entire or bifid. *Fruits* baccate or capsular. *Seeds* trigonous to rounded or reniform, sometimes with cavity at hilum, smooth or with minute striae.

Distribution: Africa, Madagascar, Asia, Malesia, Pacific, South America.

Notes —1. The genus *Cicca* is here reinstated, but considerably expanded in comparison to its original circumscription. This genus was created because the type species was very different from known *Phyllanthus* species. Based on fruit morphology, this genus has also been mixed with species of *Emblica* and *Margaritaria*. In our treatment, we consider a wider circumscription that includes former *Phyllanthus* subgenera *Anesonemoides*, *Betsileani* and *Menarda* as these were shown to be closely related (see Bouman *et al.* 2020; supplementary fig. 1). This clade was found to be sister to the diverse genus *Dendrophyllanthus* here (but see Kawakita *et al.* 2009).

2. The monotypic section *Ebolowani* was placed by Brunel (1987) in *Phyllanthus* subgenus *Ceramanthus* (here genus *Cathetus*) on the basis of a vague similarity in exine morphology. However, this species has phyllanthoid branching (vs non-phyllanthoid in the genus *Cathetus*) and staminate flowers with free stamens (connate in *Cathetus* subgenus *Cathetus*). The anther shape of *Cicca letouzeyanus* differs considerably from *Cathetus* subgenus *Macraea*, therefore we consider placing this species in *Cathetus* to be incorrect. There is no species in Africa with a close morphological affinity to *Cicca letouzeyanus*. A macroreticulate exine is also found in some species of *Moeroris*, but the species of that genus usually have connate

stamens (or free in *Moeroris* subgenus *Tenellanthus*, but then the flower is usually 5-merous). Free stamens and a small-tree like habit is more common in the genus *Cicca*. However, the exact subgenus for *C. letouzeyanus* is unclear, so we transfer this species to the genus *Cicca* without any subgeneric placement. If the species is shown to be phylogenetically distinct, section *Ebolowani* could be reinstated again.

Included, but further unplaced species and taxonomic changes (3 spp.):
Cicca analamerae (Leandri 1957: 225) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus analamerae* Leandri.
Cicca letouzeyanus (Brunel 1987: 409) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus letouzeyanus* Jean F.Brunel.
Cicca vergens (Baillon *in* Grandidier 1892: pl. 225) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vergens* Baill.

Cicca L. subgenus **Anisonemoides** (Jean F.Brunel) R.W.Bouman, *comb. nov.*

Phyllanthus L. subgenus *Anisonemoides* (Jean F.Brunel) Ralimanana & Hoffmann (2014: 267). — *Phyllanthus* L. subgenus *Kirganelia* (A.Juss.) Kurz section *Anisonemoides* Brunel (1987: 276). — Type: *Phyllanthus bojerianus* (Baill.) Müll.Arg. (based on *Kirganelia bojeriana* Baill.) = *Cicca bojeriana* (Baill.) R.W.Bouman.

Diagnostic features: Shrubs, subshrubs or small trees, monoecious or dioecious, branching phyllanthoid, branchlets (bi)pinnatiform. *Brachyblasts* absent (rarely present). *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* distichous. *Inflorescences* axillary, unisexual fascicles, rarely bisexual, not on separate branchlets. *Staminate flowers*: sepals (4)5(6); disc glands (4)5(6); stamens (2–4)5(6), filaments free or inner ones tending to be fused, anthers dehiscing longitudinally, connectives non-apiculate; pollen 3-colporate or 3-syncolporate, colpi monoporate, exine macro- or microreticulate. *Pistillate flowers*: sepals 5 or 6; disc entire; ovary 3-locular; styles absent or present; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or faintly longitudinally striate. *Distribution*: Africa, Madagascar.

Included species and taxonomic changes (13 spp.):
Cicca ambatovolana (Leandri 1938: 191) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ambatovolanus* Leandri.
Cicca ankarana (Leandri 1934: 543) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ankarana* Leandri.
Cicca bemangidiensis (Ralimanana *in* Ralimanana & Hoffmann 2014: 285) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bemangidiensis* Ralim.
Cicca bojeriana (Baillon 1861: 47) R.W.Bouman, *comb. nov.* Basionym: *Kirganelia*

bojeriana Baill., synonym: *Phyllanthus bojerianus* (Baill.) Müll.Arg. (1866: 343).

Cicca gordonii (Ralimanana *in* Ralimanana & Hoffmann 2014: 276) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gordonii* Ralim. & Petra Hoffm.

Cicca goudotiana (Baillon 1861: 62) R.W.Bouman, *comb. nov.* Basionym: *Menarda goudotiana* Baill., homotypic synonym: *Phyllanthus goudotianus* (Baill.) Müll. Arg. (1863: 8).

Cicca humbertiana (Leandri 1938: 194) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus humbertianus* Leandri.

Cicca iratsiensis (Leandri 1938: 193) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus iratsiensis* Leandri.

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

Cicca mananarensis (Leandri 1957: 230) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mananarensis* Leandr.

Cicca mantadiensis (Ralimanana & Hoffmann 2014: 280) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mantadiensis* Ralim. & Petra Hoffm.

Cicca multiflora (Poiret 1804: 229) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus multiflorus* Poir.

Cicca obdeltophylla (Leandri 1957: 232) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus obdeltophyllus* Leandri.

Cicca L. subgenus **Betsileani** (Jean F.Brunel) R.W.Bouman, *comb. nov.*

Phyllanthus L. subgenus *Macraea* (Wight) Jean F.Brunel subsection *Betsileani* Brunel (1987: 299). — *Phyllanthus* L. subgenus *Betsileani* (Jean F.Brunel) Ralimanana & Hoffmann (2011: 338). —Type: *Phyllanthus betsileanus* Leandri = *Cicca betsileana* (Leandri) R.W.Bouman.

Diagnostic features: Herbs or shrubs, monoecious or dioecious, branching non-phyllanthoid. *Brachyblasts* absent. *Leaves* spirally arranged at basal nodes, becoming distichous in distal nodes. *Inflorescences* axillary, unisexual fascicles, found on all axes. *Staminate flowers*: sepals (5 or) 6; disc glands (5 or) 6, free; stamens 3, filaments free, anthers dehiscing longitudinally, connectives non-apiculate; pollen perisyncolporate, exine reticulate. *Pistillate flowers*: sepals (5 or) 6; disc entire and lobed; ovary 3-locular; styles absent; stigmas bifid. *Fruits* capsules. *Seeds* trigonous, smooth or faintly longitudinally striate.
Distribution: Madagascar.

Included species and taxonomic changes (3 spp.):

Cicca bathiana (Leandri 1933: 371) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bathianus* Leandri.

Cicca betsileana (Leandri 1933: 372) R.W.Bouman, *comb. nov.* Basionym:

Phyllanthus betsileanus Leandri.

Cicca philippioides (Leandri 1933: 373) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus philippioides* Leandri.

Cicca L. subgenus **Cicca**

Cicca L. subgenus *Cicca*: Literature and type as under the genus.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, sometimes specialized in vegetative and floriferous branchlets. *Brachyblasts* present or absent. *Cataphyllary stipules* triangular or spinescent, indurate, base not auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, sometimes on specialized branchlets. *Staminate flowers*: sepals 4–6; disc glands 4–6, sometimes absent; stamens 2–6, filaments free, basifixed or connate, anthers dehiscing longitudinally, vertically, connectives non-apiculate; pollen: exine reticulate. *Pistillate flowers:* sepals 4–6; disc entire or segmented; ovary 2–4-locular; styles absent; stigmas bifid. *Fruits* baccate or capsular. *Seeds* trigonous or rounded, sometimes with a cavity at hilum, smooth or with minute striae.
Distribution: Africa, mainland Asia and South America.
Notes —1. Subgenus *Cicca* is distributed in Africa and the Neotropics and has one of the more complicated taxonomic histories. Species of subgenus *Cicca* have been treated in various genera, including *Margaritaria*, *Emblica* and *Phyllanthus* subgenus *Kirganelia* (Webster 2001b). Kathriarachchi *et al.* (2006), showed it to be part of a clade distinct from other species of *Kirganelia*, but related to section *Chorisandra*. The African section *Omphacodopsis* is related to sections *Cicca* and *Chorisandra* (Supplementary Fig. 1). All of these sections are characterized by the presence of (usually) leafless branches with the inflorescences (also called cauliflorous panicles: Webster 1957). They also all have staminate flowers with free stamens, but the number of stamens and sepals differ between sections. Inflorescences and baccate fruits are also found in *Kirganelia*, which complicates the distinction between these two groups, but these can differ considerably in size or locule number.
2. Three sections are included in this treatment: *Chorisandra*, *Cicca*, and *Omphacodopsis*.

Cicca L. subgenus **Cicca** section **Chorisandra** (Wight) R.W.Bouman, *comb. nov.*

Chorisandra Wight (1853: 12, pl. 1994), nom. illeg., non *Chorizandra* Brown (1810: 221). — *Phyllanthus* subgenus *Kirganelia* (A.Juss.) Kurz section *Chorisandra* (Wight) Müller (1863: 2, 6 as '*Chorizandra*'); (1866: 333); Pax & Hoffmann (1921: 22); (1931: 61); Webster (1957: 52); (1997: 216). — *Chorizonema* Brunel

(1987: 256). — Type: *Chorisandra pinnata* Wight (= formerly *Phyllanthus pinnatus* (Wight) G.L.Webster) = *Cicca pinnata* (Wight) R.W.Bouman.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles. *Staminate flowers*: sepals 4–6; disc glands 4–6; stamens 2 (*C. kidna* (Challen & Petra Hoffm.) R.W.Bouman) or 6, filaments free, basifixed or connate (*C. kidna*); anthers dehiscing longitudinally, vertically. *Pistillate flowers*: sepals 4 or 5 (*C. kidna*) or 6 (*C. pinnata* (Wight) R.W.Bouman & *C. orientalis* (Craib) R.W.Bouman); disc entire; ovary 2- or 3-locular; styles absent; stigmas usually 3, bifid. *Fruits* baccate. *Seeds* trigonous, with cavity at hilum, smooth.
Distribution: Africa, mainland Asia.
Note —Brunel (1987) raised section *Chorisandra* to generic level, but opted to use the name *Chorizonema*, since the generic name *Chorisandra* was previously used in Cyperaceae. Chantaranothai (2007) reported that *C. orientalis* has an entire disc in the staminate flower, although this needs to be corroborated.

Included species and taxonomic changes (4 spp.):

Cicca coluteoides (Baillon ex Müller 1866: 335) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus coluteoides* Baill. ex Müll.Arg.

Cicca kidna (Challen & Hoffmann 2011: 935) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kidna* Challen & Petra Hoffm.

Cicca orientalis (Craib 1914: 285) R.W.Bouman, *comb. nov.* Basionym: *Chorisandra orientalis* Craib, homotypic synonym: *Phyllanthus orientalis* (Craib) Airy Shaw (1971: 495).

Cicca pinnata (Wight 1853: 13) R.W.Bouman, *comb. nov.* Basionym: *Chorisandra pinnata* Wight, homotypic synonym: *Phyllanthus pinnatus* (Wight) Webster (1957: 52).

Cicca L. subgenus **Cicca** section **Cicca**

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

Phyllanthus L. section *Cicca* (L.) Müller subsection *Eucicca* Müller (1863: 50), nom. inval.; (1866: 413). — *Phyllanthus* subgenus *Kirganelia* (A.Juss.) Kurz section *Cicca* (L.) Webster subsection *Cheramella* Kuntze in Post & Kuntze(1904: 434). — Type: *Phyllanthus acidus* (L.) Skeels = *Cicca acida* (L.) Merr.

Aporosella Chodat (1905: 488). — *Phyllanthus* L. subgenus *Cicca* (L.) G.L.Webster section *Aporosella* (Chodat) Webster (1957: 72). — *Phyllanthus* subgenus *Kirganelia* (A.Juss.) Kurz section *Cicca* (L.) Webster subsection *Aporosella* (Chodat) Webster (2001b: 381). —Type: *Phyllanthus chacoensis* Morong = *Cicca chacoensis* (Morong) R.W.Bouman.

Diagnostic features: Trees, rarely shrubs, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, on separate branchlets without leaves. *Staminate flowers*: sepals 4–6; disc glands 4–6 or absent; stamens 3 or 4 (rarely 2 or 5), filaments free; anthers dehiscing more or less vertically; pollen 3-syncolporate, exine reticulate. *Pistillate flowers*: sepals 4; disc lobed or segmented; staminodes sometimes present; ovary 2–4-locular; styles absent or present, short; stigmas bifid. *Fruits* woody or drupaceous, indehiscent. *Seeds* trigonous, smooth. *Distribution*: South America and one widely cultivated species of unknown origin. *Note* —Two former subsections of *Phyllanthus* section *Cicca* are here placed in synonymy. These subsections were upheld by Webster (1957) to distinguish the type species from other species of section *Cicca*. The species of both subsections were previously only distinguished by their leaf shape and whether they were monoecious (subsection *Cheramella* Kuntze) or dioecious (subsection *Aporosella* (Chodat) G.L.Webster). Section *Omphacodopsis* (Jean F.Brunel) R.W.Bouman is closely related to section *Cicca* and species of both sections are characterized by specialized floriferous branchlets and staminate flowers with free stamens (some exceptions), but they differ in fruit morphology.

Included species and taxonomic changes (3 spp.):

Cicca acida (L.) Merrill (1917: 314); Basionym: *Averrhoa acida* Linnaeus (1753: 428), homotypic synonym: *Phyllanthus acidus* (L.) Skeels (1909: 17).

Cicca chacoensis (Morong *in* Morong & Britton 1892: 218) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chacoensis* Morong.

Cicca elsiae (Urban 1919: 405) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus elsiae* Urb.

Cicca L. subgenus **Cicca** (L.) G.L.Webster section **Omphacodopsis** (Jean F.Brunel) R.W.Bouman, *comb. nov*.

Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Omphacodopsis* Brunel (1987: 279). — Type: *Phyllanthus physocarpus* Müll.Arg. = *Cicca physocarpa* (Müll.Arg.) R.W.Bouman.

Phyllanthus L. subgenus *Kirganelia* (A.Juss.) Kurz section *Polyanthi* Brunel (1987: 283). — Type: *Phyllanthus polyanthus* Pax = *Cicca polyantha* (Pax) R.W.Bouman.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, sometimes specialized in vegetative and floriferous branchlets. *Brachyblasts* present. *Leaves* distichous. *Inflorescences* axillary, flowers solitary or in unisexual or bisexual fascicles. *Staminate flowers*: sepals 4 or 5; disc glands 4 or 5; stamens 4 or 5, filaments free, basifixed (or connate in *C.*

delpyana), anthers dehiscing longitudinally, vertically, connectives non-apiculate. *Pistillate flowers*: sepals 4 or 5, rarely 6; disc entire; ovary 3- or 4-locular; styles absent; stigmas bifid. *Fruits* baccate, but corky. *Seeds* ovoid-trigonous, reniform or rounded, smooth or with minute striae.
Distribution: Africa.
Note —Section *Omphacodopsis* was found to be nested within section *Polyanthi* (Bouman *et al.* 2020; supplementary fig. 1). Sections *Omphacodopsis* and *Polyanthi* were originally distinguished based on differences in fruit (berry versus inflated capsule) and seed shape (reniform versus rounded). To prevent paraphyly of section *Polyanthi*, it is here subsumed in section *Omphacodopsis* on the basis of their similarity in habit, inflorescence structure and floral morphology.

Included species and taxonomic changes (6 spp.):
Cicca delpyana (Hutchinson 1913: 1047) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus delpyanus* Hutch.
Cicca engleri (Pax 1895: 236) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus engleri* Pax.
Cicca physocarpa (Müller 1864: 515) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus physocarpus* Müll.Arg.
Cicca polyantha (Pax 1899: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus polyanthus* Pax.
Cicca profusa (Brown *in* Stapf 1905: 113) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus profusus* N.E.Br.
Cicca schliebenii (Mansfeld ex Radcliffe-Smith 1981: 772) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus schliebenii* Mansf. ex Radcl.-Sm.

Cicca L. subgenus **Menarda** (Comm. ex A.Juss.) R.W.Bouman, *comb. nov*.

Menarda Comm. ex Jussieu (1824: 23, 109); Baillon (1858: 608); Baillon (1861: 46); Baillon (1862b: 231). — *Phyllanthus* L. section *Menarda* (Comm. ex A.Juss.) Müller (1863: 2, 7); (1866: 334); Pax & Hoffmann (1931: 62); Brunel (1987: 269). — *Phyllanthus* L. subgenus *Menarda* (Comm. ex A.Juss.) Ralimanana & Hoffmann (2014: 296). —Type: *Menarda cryptophila* Comm. ex A.Juss. (formerly *Phyllanthus cryptophilus* (Comm. ex A.Juss.) Müll.Arg.) = *Cicca cryptophila* (Comm. ex A.Juss.) R.W.Bouman.
Phyllanthus L. subgenus *Anisonemoides* (Jean F.Brunel) Ralimanana & Hoffmann section *Pseudogomphidium* Ralimanana & Cable (2020: 3). —Type: *Phyllanthus marojejiensis* (Leandri) Petra. Hoffm. & McPherson. = *Cicca marojejiensis* (Leandri) R.W.Bouman.

Diagnostic features: Subshrubs or shrubs, monoecious, branching phyllanthoid, branchlets pinnatiform (to further ramified with leaves at base of ultimate

branches), sometimes two opposite branches from same node. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* opposite, sometimes sub-opposite, or alternate. *Inflorescences* axillary, unisexual or bisexual fascicles, not on separate branchlets. *Staminate flowers*: sepals 5 (-6); disc glands 5, free, globose, reniform or absent; stamens 3–5, filaments free or fused, anthers dehiscing longitudinally, vertically, connectives (non-)apiculate; pollen 3- or 4-colporate, colpi diploporate, exine perforate to microreticulate. *Pistillate flowers*: sepals 5 (or 6); disc entire, lobed or reduced; ovary 3-locular, globose or depressed globose; styles present or absent; stigmas entire or bifid for up to 2/3 of the length. *Fruits* capsules. *Seeds* trigonous, smooth or thinly longitudinally striate.
Distribution: Madagascar.
Notes —1. Ralimanana & Hoffmann (2014) listed the wrong author of the name *Menarda*. This should remain de Jussieu, who first described it (de Jussieu 1824) as a separate genus, instead of Müller, who reduced it to a section (Müller 1863).
2. Baillon (1861b) strangely treats subgenus *Menarda* both as a separate genus (1861: 46), but also describes some species in *Phyllanthus* section *Menarda* (1862a: 62).
3. *Phyllanthus* subgenus *Anesonemoides* section *Pseudogomphidium* was created in the fourth part of the taxonomic revision of *Phyllanthus* in Madagascar (Ralimanana & Cable 2020). A new section was deemed necessary as the species that were originally placed in *Phyllanthus* subgenus *Gomphidium* (Ralimanana & Hoffmann 2011) were found to be closer to other species from Madagascar in the phylogenetic tree from Kawakita *et al.* (2009). However, if retained, this section would be paraphyletic as *Phyllanthus* subgenus *Menarda* was found to be the nested within this clade of species (Bouman *et al.* 2021; Supplementary Fig. 1).

Included species and taxonomic changes (13 spp.):

Cicca ankaratrae (Leandri 1957: 214) R.W.Bouman, *comb. nov.* Basionym: *Glochidion ankaratrae* Leandri, homotypic synonym: *Phyllanthus ankaratrae* (Leandri) Hoffmann & McPherson (2003: 308).

Cicca ankirindrensis (Ralimanana & Cable 2020: 3) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ankirindrensis* Ralim. & Cable.

Cicca bernieriana (Baillon ex Müller 1866: 361) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bernierianus* Baill. ex Müll.Arg.

Cicca coodei (Ralimanana & Hoffmann 2014: 298) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus coodei* Ralim. & Petra Hoffm.

Cicca cryptophila (Commerson ex de Jussieu 1824: 109) R.W.Bouman, *comb. nov.* Basionym: *Menarda cryptophila* Comm. ex A.Juss., homotypic synonym: *Phyllanthus cryptophilus* (Comm. ex A.Juss.) Müller (1863: 8).

Cicca humbertii (Leandri 1957: 215) R.W.Bouman, *comb. nov.* Basionym: *Glochidion humbertii* Leandri, homotypic synonym: *Phyllanthus humbertii*

(Leandri) Hoffman & McPherson (2003: 308).

Cicca lichenisilvae (Leandri 1937: 29) R.W.Bouman, *comb. nov.* Basionym: *Glochidion lichenisilvae* Leandri, homotypic synonym: *Phyllanthus lichenisilvae* (Leandri) Hoffmann & McPherson (2003: 308).

Cicca marojejiensis (Leandri 1957: 215) R.W.Bouman, *comb. nov.* Basionym: *Glochidion marojejiense* Leandri, homotypic synonym: *Phyllanthus marojejiensis* (Leandri) Hoffmann & McPherson (2003: 308).

Cicca oreichtitus (Leandri 1934: 450) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus monticola* Leandri, nom. illeg., non *Phyllanthus monticola* Hutchinson & Dalziel (1928: 291), homotypic synonym: *Phyllanthus oreichtitus* Leandri (1935: 24).

Cicca perrieri (Leandri 1934: 606) R.W.Bouman, *comb. nov.* Basionym: *Glochidion perrieri* Leandri, homotypic synonym: *Phyllanthus perrieri* (Leandri) Hoffman & McPherson (2003: 308).

Cicca razakamalalae (Ralimanana & Cable 2020: 6) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus razakamalalae* Ralim. & Cable.

Cicca sambiranensis (Leandri 1934: 451) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sambiranensis* Leandri.

Cicca vakinankaratrae (Leandri 1957: 233) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus vakinankaratrae* Leandri.

Dendrophyllanthus S.Moore

Dendrophyllanthus Moore (1921: 395). — Type: *Dendrophyllanthus comptonii* S.Moore (= formerly *Phyllanthus moorei* M.Schmid).

Phyllanthus L. section *Gomphidium* Baillon (1862b: 234); Müller (1866: 319); Schmid (1991: 64). — *Phyllanthus* L. section *Paragomphidium* Müller (1863: 3, 14), nom. superfl; (1866: 351). — *Glochidion* J.R.Forst. & G.Forst. section *Gomphidium* (Baill.) Müller (1863: 58, 70); Pax & Hoffmann (1931: 58). — *Phyllanthus* L. subgenus *Gomphidium* (Baill.) Webster (1967b: 338); (1971: 92). —Lectotype (selected by Webster 1967b): *Phyllanthus chamaecerasus* Baill. = *Dendrophyllanthus chamaecerasus* (Baill.) R.W.Bouman.

Diagnostic features: Herbs, shrubs or trees, monoecious, branching phyllanthoid, branchlets (bi)pinnatiform, glabrous or pubescent. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular. *Leaves* distichous, sometimes opposite, branchlets sometimes with a single leaf. *Inflorescences* axillary, unisexual, rarely bisexual fascicles, sometimes paniculate but generally not on separate specialized branchlets. *Staminate flowers*: sepals 5 or 6, usually in two whorls, inner whorl often longer than androecium; disc entire or 3 or 6 massive glands or absent; stamens 3–20, filaments free or connate, anthers dehiscing vertically to obliquely to horizontally, connectives sometimes apiculate;

pollen 3-colporate or 3-syncolporate, exine reticulate, vermiculate, pilate or ± vermiculate. *Pistillate flowers*: sepals 5 or 6, in two whorls, often differing in length, one whorl possibly accrescent or reduced to absent; disc entire, segmented or absent; ovary 3–5-locular; style present or absent; stigma tips entire or bifid. *Fruits* capsules. *Seeds* trigonous, smooth.
Distribution: Malesia, Australia and Pacific.

Included, but further unplaced species and taxonomic changes (1 sp.):
Dendrophyllanthus ciliaris (Baillon 1876: 373) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ciliaris* Baill.

Dendrophyllanthus S.Moore section **Dendrophyllanthus**

Dendrophyllanthus S.Moore section *Dendrophyllanthus*: Literature and type as under the genus.
Phyllanthus L. section *Phyllocalyx* Baillon (1862b: 236). — *Glochidion* J.R.Forst. & G.Forst. section *Physoglochidion* Müller (1863: 58, 71), *nom. superfl.*; Pax & Hoffmann (1931: 58). —*Phyllanthus* L. section *Physoglochidion* (Müll.Arg.) Müller (1866: 318), *nom. superfl.* — *Phyllanthus* L. subgenus *Gomphidium* (Baill.) G.L.Webster section *Gomphidium* Baill. subsection *Physoglochidion* (Müll.Arg.) Bouman in Bouman *et al.* (2018: 170). — Type: *Phyllanthus faguetii* Baill. = *Dendrophyllanthus faguetii* (Baill.) R.W.Bouman.
Leichhardtia Mueller (1876: 67), nom. illeg., non *Leichardtia* Brown (1849: 81). — *Phyllanthus* L. section *Leichhardtia* (F.Muell.) Diels (1931: 308). — Type: *Leichhardtia clamboides* F.Muell. (formerly *Phyllanthus clamboides* (F.Muell.) Diels) = *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman.
Nymania Schumann (1905: 291), nom. illeg., non *Nymania* Lindberg (1868: 290). — *Phyllanthus* L. subgenus *Gomphidium* (Baill.) G.L.Webster section *Nymania* (K.Schum.) Smith (1912: 781). —Type: *Nymania insignis* K.Schum (= formerly a synonym of *Phyllanthus schumannianus* L.S.Sm.) = *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman.
Hexaspermum Domin (1927: 869)). — Type: *Hexaspermum paniculatum* (Oliv.) Domin (= based on *Phyllanthus paniculatus* Oliv.; formerly synonyms of *Phyllanthus clamboides* (F.Muell.) Diels) = *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman.

Diagnostic features: Shrubs or trees, monoecious, branching phyllanthoid, branchlets (bi)pinnatiform, glabrous or pubescent. *Brachyblasts* absent. *Leaves* distichous, sometimes opposite. *Inflorescences* axillary, mostly unisexual, some bisexual fascicles, or panicles. *Staminate flowers:* sepals 6, in two whorls, inner whorl often longer than androecium; disc 3 massive (bilobed) glands (rarely 6); stamens 3, filaments free or connate, anthers dehiscing vertically to obliquely,

connectives apiculate; pollen oblate, 3-colporate or 3-syncolporate, exine rugulose-reticulate, vermiculate, pilate or ± vermiculate. *Pistillate flowers:* sepals 6, in two whorls, often differing in length, one whorl sometimes accrescent or reduced to absent; disc entire, sometimes very small to absent; ovary 3-locular; styles present or absent; stigmas entire (rarely bifid). *Fruits* capsules. *Seeds* trigonous.
Distribution: Malesia, Australia and Pacific.
Notes —1. McPherson & Schmid (1991) grouped many other taxa together in their informal groups 6 and 7, which correspond to *Dendrophyllanthus* sections *Dendrophyllanthus* and *Leptonema* (Baill.) R.W.Bouman. Any previously defined subsections were not treated separately by McPherson & Schmid (1991) since they are morphologically very similar. *Phyllanthus* subsection *Physoglochidion* was represented by only one species in the phylogenetic study of Bouman *et al.* (2021), if retained it would necessitate the recognition of several other subsections. As this might result in a confusing classification with morphologically very similar subsections, we have opted to subsume subsection *Physoglochidion* within *Dendrophyllanthus* section *Dendrophyllanthus*.
2. *Phyllanthus* subgenus *Gomphidium* section *Nymania* (K.Schum) J.J.Sm. was found to be paraphyletic with the rest of *Phyllanthus* section *Gomphidium* nested within (Bouman *et al.* 2021). Both sections have the same number of stamens and disc glands, but differ slightly in the fusion of the filaments and some pollen characters (Airy Shaw 1980a). However, species with free and connate filaments occur in the previous classification of *Phyllanthus* section *Nymania* (e.g. *D. tenuirhachis* (J.J.Sm.) R.W.Bouman: free; and *D. cuscutiflorus* (S.Moore) R.W.Bouman: connate). Bipinnatiform branchlets also occur in both sections, resulting in almost no distinction between the groups and hence they are here combined.
3. Some species with six staminate disc glands from the Philippines were shown to belong to the genus *Emblica* (e.g., *E. rufuschaneyi* (Welzen, R.W.Bouman & Ent) R.W.Bouman; Bouman *et al.* 2021), which casts some doubt on the placement of similar species, such as *D. rheophila* (Airy Shaw) R.W.Bouman; this requires further study.

Included species and taxonomic changes (88 spp.):
Dendrophyllanthus acinacifolius (Airy Shaw & Webster 1971: 95) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus acinacifolius* Airy Shaw & G.L.Webster.
Dendrophyllanthus actephilifolius (Smith 1917: 543) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus actephilifolius* J.J.Sm.
Dendrophyllanthus amicorus (Webster 1986: 100) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amicorum* G.L.Webster.
Dendrophyllanthus amieuensis (Guillaumin 1962: 242) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus amieuensis* Guillaumin.
Dendrophyllanthus aphanostyla (Airy Shaw & Webster 1971: 106) R.W.Bouman,

comb. nov. Basionym: *Phyllanthus aphanostylus* Airy Shaw & G.L.Webster.

Dendrophyllanthus apiculatus (Merrill 1920: 540) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus apiculatus* Merr.

Dendrophyllanthus ardisianthus (Airy Shaw & Webster 1971: 94) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ardisianthus* Airy Shaw & G.L.Webster.

Dendrophyllanthus avanguiensis (Schmid 1991: 182) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus avanguiensis* M.Schmid.

Dendrophyllanthus balansanus (Guillaumin 1929: 4) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus balansanus* Guillaumin.

Dendrophyllanthus bourgeoisii (Baillon 1862b: 235) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bourgeoisii* Baill.

Dendrophyllanthus buxoides (Guillaumin 1929: 6) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus buxoides* Guillaumin.

Dendrophyllanthus calcicola (Schmid 1991: 118) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus calcicola* M.Schmid.

Dendrophyllanthus castus (Moore 1921: 401) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus castus* S.Moore.

Dendrophyllanthus caudatus (Müller 1866: 321) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caudatus* Müll.Arg.

Dendrophyllanthus chamaecerasus (Baillon 1862b: 235) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chamaecerasus* Baill.

Dendrophyllanthus clamboides (Mueller 1876: 68) R.W.Bouman, *comb. nov.* Basionym: *Leichhardtia clamboides* F.Muell., homotypic synonym: *Phyllanthus clamboides* (F.Muell.) Diels (1931: 309).

Dendrophyllanthus cordatulus (Robinson 1909: 76) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cordatulus* C.B.Rob.

Dendrophyllanthus cornutus (Baillon 1862b: 236) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cornutus* Baill.

Dendrophyllanthus comptonii Moore (1921: 395), non *Phyllanthus comptonii* Moore 1921: 398), homotypic synonym: *Phyllanthus moorei* Schmid (1991: 159).

Dendrophyllanthus cuscutiflorus (Moore 1905: 148) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cuscutiflorus* S.Moore.

Dendrophyllanthus dzumacensis (Schmid 1991: 105) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dzumacensis* M.Schmid.

Dendrophyllanthus effusus (Moore 1923: 45) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus effusus* S.Moore.

Dendrophyllanthus faguetii (Baillon 1862b: 237) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus faguetii* Baill.

Dendrophyllanthus finschii (Schumann 1887: 205) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus finschii* K.Schum.

Dendrophyllanthus flaviflorus (Schumann & Lauterbach 1900: 388) R.W.Bouman, *comb. nov.* Basionym: *Actephila flaviflora* K.Schum. & Lauterb., homotypic synonym: *Phyllanthus flaviflorus* (K.Schum. & Lauterb.) Airy Shaw (1969: 39).

Dendrophyllanthus frodinii (Airy Shaw 1972: 74) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus frodinii* Airy Shaw.

Dendrophyllanthus gjellerupi (Smith 1912: 780) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus gjellerupi* J.J.Sm.

Dendrophyllanthus glochidioides (Elmer 1911: 1302) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus glochidioides* Elmer.

Dendrophyllanthus helenae (M.Schmid 1991: 77) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus helenae* M.Schmid.

Dendrophyllanthus heterodoxus (Müller *in* de Candolle 1866: 321) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus heterodoxus* Müll.Arg.

Dendrophyllanthus houailouensis (Schmid 1991: 93) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus houailouensis* M.Schmid.

Dendrophyllanthus insulae-japen (Airy Shaw 1978: 37) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus insulae-japen* Airy Shaw.

Dendrophyllanthus jaffrei (Schmid 1991: 113) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus jaffrei* M.Schmid.

Dendrophyllanthus jaubertii (Vieillard ex Guillaumin 1929: 9) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus jaubertii* Vieill. ex Guillaumin.

Dendrophyllanthus koghiensis (Guillaumin 1929: 10) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus koghiensis* Guillaumin.

Dendrophyllanthus koniamboensis (Schmid 1991: 136) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus koniamboensis* M.Schmid.

Dendrophyllanthus kostermansii (Airy Shaw 1974: 296) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kostermansii* Airy Shaw.

Dendrophyllanthus kouaouaensis (Schmid 1991: 114) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kouaouaensis* M.Schmid.

Dendrophyllanthus koumacensis (Guillaumin 1965: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus koumacensis* Guillaumin.

Dendrophyllanthus macphersonii (Schmid 1991: 142) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus macphersonii* M.Schmid.

Dendrophyllanthus mangenotii (Schmid 1991: 156) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mangenotii* M.Schmid.

Dendrophyllanthus merinthopodus (Diels 1931: 310) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus merinthopodus* Diels.

Dendrophyllanthus montis-fontius (Schmid 1991: 78) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus montis-fontium* M.Schmid.

Dendrophyllanthus mouensis (Schmid 1991: 104) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mouensis* M.Schmid.

Dendrophyllanthus natoensis (Schmid 1991: 171) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus natoensis* M.Schmid.

Dendrophyllanthus ningaensis (Schmid 1991: 144) R.W.Bouman, *comb. nov.*

Basionym: *Phyllanthus ningaensis* M.Schmid.

Dendrophyllanthus nothisii (Schmid 1991: 179) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nothisii* M.Schmid.

Dendrophyllanthus ovatifolius (Smith 1920: 390) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ovatifolius* J.J.Sm.

Dendrophyllanthus pancherianus (Baillon 1862b: 235) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pancherianus* Baill.

Dendrophyllanthus papuanus (Gage 1917: 479) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus papuanus* Gage.

Dendrophyllanthus paucitepalus (Schmid 1991: 140) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus paucitepalus* M.Schmid.

Dendrophyllanthus pergracilis (Gillespie 1932: 18) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pergracilis* Gillespie.

Dendrophyllanthus petchikaraensis (Schmid 1991: 90) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus petchikaraensis* M.Schmid.

Dendrophyllanthus pilifer (Schmid 1991: 120) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pilifer* M.Schmid.

Dendrophyllanthus pindaiensis (Schmid 1991: 183) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pindaiensis* M.Schmid.

Dendrophyllanthus pinjenensis (Schmid 1991: 92) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pinjenensis* M.Schmid.

Dendrophyllanthus platycalyx (Müller *in* de Candolle 1866: 318) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus platycalyx* Müll.Arg.

Dendrophyllanthus poliborealis (Airy Shaw 1978: 36.) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poliborealis* Airy Shaw.

Dendrophyllanthus polygynus (Schmid 1991: 97) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus polygynus* M.Schmid.

Dendrophyllanthus poueboensis (Schmid 1991: 154) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poueboensis* M.Schmid.

Dendrophyllanthus poumensis (Guillaumin 1929: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poumensis* Guillaumin.

Dendrophyllanthus praelongipes (Airy Shaw & Webster 1971: 100) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus praelongipes* Airy Shaw & G.L.Webster.

Dendrophyllanthus pterocladus (Moore 1921: 400) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pterocladus* S.Moore.

Dendrophyllanthus pulchellus (Airy Shaw 1969: 22) R.W.Bouman, *comb. nov.* Basionym *Glochidion pulchellum* Airy Shaw, homotypic synonym: *Phyllanthus stultitiae* Airy Shaw (1978: 368).

Dendrophyllanthus pullenii (Airy Shaw & Webster 1971: 105) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pullenii* Airy Shaw & G.L.Webster.

Dendrophyllanthus quintuplinervis (Schmid 1991: 148) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus quintuplinervis* M.Schmid.

Dendrophyllanthus rheophilus (Airy Shaw 1966: 385) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rheophilus* Airy Shaw.

Dendrophyllanthus rosselensis (Airy Shaw & Webster 1971: 103) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rosselensis* Airy Shaw & G.L.Webster.

Dendrophyllanthus rubriflorus (Smith 1912: 781) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rubriflorus* J.J.Sm.

Dendrophyllanthus rupiinsularis (Hosokawa 1935: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rupiinsularis* Hosok.

Dendrophyllanthus salomonis (Airy Shaw 1978: 368) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus salomonis* Airy Shaw.

Dendrophyllanthus securinegoides (Merrill 1914: 490) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus securinegoides* Merr.

Dendrophyllanthus smithianus (Webster 1986: 99) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus smithianus* G.L.Webster.

Dendrophyllanthus stenophyllus (Guillaumin 1929: 17) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus stenophyllus* Guillaumin.

Dendrophyllanthus stipitatus (Schmid 1991: 178) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus stipitatus* M.Schmid.

Dendrophyllanthus tabularis (Airy Shaw 1980b: 598) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tabularis* Airy Shaw.

Dendrophyllanthus tagulae (Airy Shaw & Webster 1971: 102) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tagulae* Airy Shaw & G.L.Webster.

Dendrophyllanthus tangoensis (Schmid 1991: 162) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tangoensis* M.Schmid.

Dendrophyllanthus tenuipedicellatus (Schmid 1991: 98) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuipedicellatus* M.Schmid.

Dendrophyllanthus tenuirhachis (Smith 1908: t. 263) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tenuirhachis* J.J.Sm.

Dendrophyllanthus tiebaghiensis (Schmid 1991: 94) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tiebaghiensis* M.Schmid.

Dendrophyllanthus unioensis (Schmid 1991: 139) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus unioensis* M.Schmid.

Dendrophyllanthus utricularis (Airy Shaw & Webster 1971: 101) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus utricularis* Airy Shaw & G.L.Webster.

Dendrophyllanthus veillonii (Schmid 1991: 130) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus veillonii* M.Schmid.

Dendrophyllanthus vieillardii (Müller 1863: 70) R.W.Bouman, *comb. nov.* Basionym: *Glochidion vieillardii* Müll.Arg. (non *Phyllanthus vieillardii* Baillon 1862b: 236), homotypic synonym: *Phyllanthus tritepalus* Schmid (1991: 153).

Dendrophyllanthus virgultiramus (Däniker 1931: 169) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus virgultiramus* Däniker.

Dendrophyllanthus warburgii (Schumann 1905: 286) R.W.Bouman, *comb. nov.*

Basionym: *Phyllanthus columnaris* Warburg (1891: 356), nom. illeg., non *Phyllanthus columnaris* Müller (1863: 15), homotypic synonym: *Phyllanthus warburgii* K.Schum.

Dendrophyllanthus wilkesianus (Müller 1866: 396) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus wilkesianus* Müll.Arg.

Dendrophyllanthus L. section **Leptonema** (Baill.) R.W.Bouman, *comb. nov.*

Phyllanthus L. section *Leptonema* Baillon (1862b: 234). — *Glochidion* J.R.Forst. & G.Forst. section *Pentaglochidion* Müller (1863: 58, 59), nom. superfl.; Pax & Hoffmann (1931: 58). — *Phyllanthus* L. section *Pentaglochidion* (Müll. Arg.) Müller (1866: 315), nom. superfl. — *Phyllanthus* L. (informal) groupe 6: Schmid (1991: 184). — Type: *Phyllanthus kanalensis* Baill. = *Dendrophyllanthus kanalensis* (Baill.) R.W.Bouman.

Glochidion J.R.Forst. & G.Forst. section *Adenoglochidion* Müller (1863: 58); Pax & Hoffmann (1931: 58). — *Phyllanthus* L. section *Adenoglochidion* (Müll.Arg.) Müller (1866: 319). — Type: *Phyllanthus aeneus* Baill. = *Dendrophyllanthus aeneus* (Baill.) R.W.Bouman.

Phyllanthus L. section *Polyandroglochidion* Moore (1921: 402); Pax & Hoffmann (1931: 61). — Type: *Phyllanthus sylvincola* S.Moore = *Dendrophyllanthus sylvincolus* (S.Moore) R.W.Bouman.

Phyllanthus L. section *Meiandroglochidion* Moore (1921: 402); Pax & Hoffmann (1931: 61). —Type: *Phyllanthus ligustrifolius* S.Moore = *Dendrophyllanthus ligustrifolius* (S.Moore) R.W.Bouman.

Phyllanthus L. section *Eleutherogynium* Müller (1863: 4, 14). — *Glochidion* J.R.Forst. & G.Forst. section *Eleutherogynium* (Müll.Arg.) Pax & Hoffmann (1931: 58). — *Phyllanthus* L. subgenus *Gomphidium* (Baill.) G.L.Webster section *Adenoglochidion* (Müll.Arg.) Müll.Arg. subsection *Eleutherogynium* (Müll. Arg.) Webster ex Bouman *in* Bouman *et al.* (2018: 170). — Type: *Phyllanthus loranthoides* Baill. = *Dendrophyllanthus loranthoides* (Baill.) R.W.Bouman.

Glochidion J.R.Forst. & G.Forst. section *Chorizogynium* Müller (1863: 58). — Lectotype (designated by Webster 1986): *Phyllanthus macrochorion* Baill. = *Dendrophyllanthus macrochorion* (Baill.) R.W.Bouman.

Phyllanthus L. section *Heteroglochidion* Müller (1866: 319). —*Glochidion* J.R.Forst. & G.Forst. section *Heteroglochidion* (Müll.Arg.) Pax & Hoffmann (1931: 58). — Type: *Phyllanthus baladensis* Baill. = *Dendrophyllanthus baladensis* (Baill.) R.W.Bouman.

Phyllanthus L. section *Scleroglochidion* Müller (1866: 317). —*Glochidion* J.R.Forst. & G.Forst. section *Scleroglochidion* (Müll.Arg) Pax & Hoffmann (1931: 62). — Type: *Phyllanthus myrianthus* Müll.Arg. = *Dendrophyllanthus myrianthus* (Müll. Arg.) R.W.Bouman.

Diagnostic features: Herbs, shrubs to trees, monoecious, branching phyllanthoid, branchlets pinnatiform, glabrous. *Brachyblasts* absent. *Leaves* distichous, sometimes branchlets bearing only a single leaf. *Inflorescences* axillary, often bisexual fascicles. *Staminate flowers*: sepals 5, sometimes 6, not clearly biseriate; disc entire or free glands, sometimes absent; stamens 3 or 5(7—20), filaments free, inserted often on a large receptacle, anthers dehiscing vertically to horizontally, often oblique, connectives non-apiculate; pollen 3-syncolporate, exine reticulate. *Pistillate flowers:* sepals 5 or 6; disc entire or segmented, sometimes absent; ovary 3- to 5-locular; styles absent or present; stigmas entire, rarely bifid (*D. nitens* (M.Schmid) R.W.Bouman, *D. torrentium* (Müll.Arg.) R.W.Bouman). *Fruits* capsules. *Seeds* trigonous.

Distribution: Malesia, Australia and Pacific (mainly New Caledonia).

Notes —1. *Phyllanthus* section *Leptonema* is nested within a paraphyletic *Phyllanthus* section *Adenoglochidion* (Bouman *et al.* 2021) and the two groups are therefore combined and transferred as *Dendrophyllanthus* section *Leptonema*. Section *Leptonema* was originally distinguished from other groups based on its absent disc and the 5-locular ovary in the pistillate flower (Baillon 1862b). However, several species within former *Phyllanthus* section *Adenoglochidion* (specifically the former subsection *Eleutherogynium*) have a reduced or an absent disc, so the combination of these two sections is not surprising. The number of locules is variable within *Dendrophyllanthus* and also in the genus *Glochidion* and is probably related to a pollination mutualism with moths as the pollinator.

2. McPherson & Schmid (1991) adopted a broad delimitation of *Phyllanthus* section *Adenoglochidion*, which is here subsumed within section *Leptonema*. This means that sections *Polyandroglochidion* S.Moore and *Meiandroglochidion* S.Moore are also subsumed, which only alters the description in relation to the number of stamens, with the other characters, including those from pistillate flowers, overlapping. *Polyandroglochidion* was defined on the basis of its absent discs glands, the 14 free stamens, 3- or 4-locular ovary and 3 or 4 free undivided stigmas. *Phyllanthus* section *Meiandroglochidion* was defined as close to *Phyllanthus* section *Polyandroglochidion*, but differing in the presence of a disc in the staminate flowers and with fewer stamens (7‑10).

Included species and taxonomic changes (72 spp.):

Dendrophyllanthus aeneus (Baillon 1862b: 231) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus aeneus* Baill.

Dendrophyllanthus aoupinieensis Schmid 1991: 275) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus aoupinieensis* M.Schmid.

Dendrophyllanthus artensis (Schmid 1991: 242) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus artensis* M.Schmid.

Dendrophyllanthus baladensis (Baillon 1862b: 233) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus baladensis* Baill.

Dendrophyllanthus baraouaensis (Schmid 1991: 272) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baraouaensis* M.Schmid.

Dendrophyllanthus boguenensis (Schmid 1991: 286) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus boguenensis* M.Schmid.

Dendrophyllanthus bupleuroides (Baillon 1862b) 233) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bupleuroides* Baill.

Dendrophyllanthus brassii (White 1936: 81) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus brassii* C.T.White.

Dendrophyllanthus casearioides (Moore 1921: 397) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus casearioides* S.Moore.

Dendrophyllanthus caesius (Airy Shaw & Webster 1971: 90) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caesius* Airy Shaw & G.L.Webster.

Dendrophyllanthus carlottae (Schmid 1991: 258) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carlottae* M.Schmid.

Dendrophyllanthus caudatifolius (Merrill 1926: 403) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus caudatifolius* Merr.

Dendrophyllanthus cherrieri (Schmid 1991: 278) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus cherrieri* M.Schmid.

Dendrophyllanthus chrysofructa Strijk & R.W.Bouman, *nom. nov*. Basionym: *Phyllanthus valeriae* Schmid (1991: 217), nom. illeg., non *Phyllanthus valerii* Standley (1937: 619).

Dendrophyllanthus conjugatus (Schmid 1991: 279) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus conjugatus* M.Schmid.

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

Dendrophyllanthus deciduiramus (Däniker 1931: 167) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus deciduiramus* Däniker.

Dendrophyllanthus dorotheae (Schmid 1991: 300) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dorotheae* M.Schmid.

Dendrophyllanthus dumbeaensis (Schmid 1991: 200) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dumbeaensis* M.Schmid.

Dendrophyllanthus erwinii (Hunter & Bruhl 1996: 130) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus erwinii* J.T.Hunter & J.J.Bruhl.

Dendrophyllanthus favieri (Schmid 1991: 262) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus favieri* M.Schmid.

Dendrophyllanthus fimbriatitepalus (Guillaumin 1937: 300) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fimbriatitepalus* Guillaumin.

Dendrophyllanthus fractiflexus (Schmid 1991: 238) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus fractiflexus* M.Schmid.

Dendrophyllanthus francii (Guillaumin 1927: 273) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus francii* Guillaumin.

Dendrophyllanthus gneissicus (Moore 1921: 399) R.W.Bouman, *comb. nov.*

Basionym: *Phyllanthus* gneissicus S.Moore.

Dendrophyllanthus golonensis (Schmid 1991: 304) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus golonensis* M.Schmid.

Dendrophyllanthus guillauminii (Däniker 1931: 167) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus guillauminii* Däniker.

Dendrophyllanthus hypospodius (Mueller 1892: 177) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus hypospodius* F.Muell.

Dendrophyllanthus kanalensis (Baillon 1862b: 234) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kanalensis* Baill.

Dendrophyllanthus lacerosus (Airy Shaw 1980c: 386) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lacerosus* Airy Shaw.

Dendrophyllanthus lacunarius (Mueller 1855: 14) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lacunarius* F.Muell.

Dendrophyllanthus lacunellus (Airy Shaw 1980c: 387) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lacunellus* Airy Shaw.

Dendrophyllanthus ligustrifolius (Moore 1921: 402) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ligustrifolius* S.Moore.

Dendrophyllanthus longiramosus (Guillaumin 1962: 292, as '*longeramosa*') R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus longiramosus* Guillaumin.

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

Dendrophyllanthus luciliae (Schmid 1991: 269) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus luciliae* M.Schmid.

Dendrophyllanthus macrochorion (Baillon 1862b: 232) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus macrochorion* Baill.

Dendrophyllanthus mandjeliaensis (Schmid 1991: 315) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mandjeliaensis* M.Schmid.

Dendrophyllanthus margaretae (Schmid 1991: 316) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus margaretae* M.Schmid.

Dendrophyllanthus maritimus (Smith 1912: 779) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus maritimus* J.J.Sm.

Dendrophyllanthus memaoyaensis (Schmid 1991: 274) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus memaoyaensis* M.Schmid.

Dendrophyllanthus meuieensis (Schmid 1991: 249) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus meuieensis* M.Schmid.

Dendrophyllanthus montrouzieri (Guillaumin 1913: 109) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus montrouzieri* Guillaumin.

Dendrophyllanthus mooreanus R.W.Bouman, *nom. nov*. Basionym: *Phyllanthus comptonii* S.Moore (1921: 398) (non *Dendrophyllanthus comptonii* S.Moore 1921: 395).

Dendrophyllanthus moratii (Schmid 1991: 313) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus moratii* M.Schmid.

Dendrophyllanthus myrianthus (Müller 1866: 317) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus myrianthus* Müll.Arg.

Dendrophyllanthus nitens (Schmid 1991: 239) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus nitens* M.Schmid.

Dendrophyllanthus ouveanus (Däniker 1931: 168) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ouveanus* Däniker.

Dendrophyllanthus parainduratus (Schmid 1991: 228) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus parainduratus* M.Schmid.

Dendrophyllanthus parangoyensis (Schmid 1991: 250) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus parangoyensis* M.Schmid.

Dendrophyllanthus peltatus (Guillaumin 1929: 13) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus peltatus* Guillaumin.

Dendrophyllanthus pronyensis (Guillaumin 1927: 273) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pronyensis* Guillaumin.

Dendrophyllanthus pseudotrichopodus (Schmid 1991: 245) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pseudotrichopodus* M.Schmid.

Dendrophyllanthus ramosii (Quisumbing & Merrill 1928: 160) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus ramosii* Quisumb. & Merr.

Dendrophyllanthus rhodocladus (Moore 1921: 397) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rhodocladus* S.Moore.

Dendrophyllanthus rozennae (Schmid 1991: 303) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rozennae* M.Schmid.

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

Dendrophyllanthus sarasinii (Guillaumin 1929: 16) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sarasinii* Guillaumin.

Dendrophyllanthus sauropodoides (Airy Shaw 1980c: 216) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sauropodoides* Airy Shaw.

Dendrophyllanthus serpentinus (Moore 1921: 399) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus serpentinus* S.Moore.

Dendrophyllanthus sylvincola (Moore 1921: 401) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sylvincola* S.Moore.

Dendrophyllanthus tireliae (Schmid 1991: 246) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tireliae* M.Schmid.

Dendrophyllanthus tixieri (Schmid 1991: 241) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tixieri* M.Schmid.

Dendrophyllanthus torrentium (Müller 1866: 316) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus torrentium* Müll.Arg.

Dendrophyllanthus trichopodus (Guillaumin 1929: 17) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus trichopodus* Guillaumin, Arch. Bot. Mém. 2(3: (.

Dendrophyllanthus umbricolus (Guillaumin 1929: 18) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus umbricola* Guillaumin.

Dendrophyllanthus unifoliatus (Schmid 1991: 198) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus unifoliatus* M.Schmid.
Dendrophyllanthus verrucicaulis (Airy Shaw 1978: 35) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus verrucicaulis* Airy Shaw.
Dendrophyllanthus vespertilio (Baillon 1862b: 233) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus vespertilio* Baill.
Dendrophyllanthus vulcani (Guillaumin 1962: 248) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus vulcani* Guillaumin.
Dendrophyllanthus yaouhensis (Schlechter 1906: 146) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus yaouhensis* Schltr.
Dendrophyllanthus yvettae (Schmid 1991: 309) R.W.Bouman, *comb. nov.*
Basionym: *Phyllanthus yvettae* M.Schmid.

Clade G — Figs. 1, 2L & M (supplementary fig. 1)

Emblica Gaertn.

Emblica Gaertner (1790: 122); de Jussieu (1824: 20); Wight (1852: t. 1896); Ridley (1924: 217); Das (1940: 159). — *Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz (1873: 238); Webster (1967a: 194). — *Phyllanthus* L. section *Emblica* (Gaertn.) Baillon (1858: 626); Müller (1863: 3, 14); (1866: 351); Hooker (1887: 286); Boerlage (1900: 212); Pax & Hoffmann (1931: 64); Webster (1997: 219). — Type: *Emblica officinalis* Gaertn. (= formerly *Phyllanthus emblica* L.).
Dichelactina Hance *in* Walpers (1852: 375). — Type: *Dichelactina nodicaulis* Hance = *Emblica officinalis* Gaertn.
Phyllanthus L. section *Typhophyllanthus* Kuntze subsection *Urinaria* Kuntze *in* Post & Kuntze (1904: 434). — *Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz section *Urinaria* (Kuntze) Webster (1955: 51); (1957: 192); (1970: 65); (1997: 227); Schmid (1991: 54); Ralimanana & Hoffmann *in* Ralimanana *et al.* (2013: 555). — *Phyllanthus* L. subgenus *Emblica* (Gaertn.) Kurz section *Urinaria* G.L.Webster subsection *Urinaria* (Kuntze) Haicour & Rossignol *in* Rossignol *et al.* (1987: 1857). — Type: *Phyllanthus urinaria* L. = *Emblica urinaria* (L.) R.W.Bouman.
Phyllanthus L. subgenus *Emblica* (Gaertn.) Kurz section *Emblica* (Gaertn.) Baill. subsection *Baeobotryoides* Brunel (1987: 232). — Type: *Phyllanthus baeobotryoides* Wall. ex Müll.Arg. = *Emblica baeobtoryoida* (Wall. ex Müll.Arg.) R.W.Bouman.

Diagnostic features: Herbs, shrubs or trees, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* sometimes present. *Cataphyllary stipules* ovate-triangular, membranous or indurate, base (not) auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, sometimes paniculate. *Staminate flowers:* sepals 6; disc glands 6, alternating with sepals; stamens 3, filaments connate, anthers elongate, dehiscing vertically, connectives sometimes apiculate; pollen prolate to spheroidal, 4- or 5-colporate or 5-brevisulcate, colpi monoporate, exine reticulate; pistillode absent. *Pistillate flowers:* sepals 6; disc entire; ovary 3-locular, sometimes tuberculate in herbaceous species; styles present; stigmas bifid. *Fruits* capsules or drupes. *Seeds* trigonous, smooth or with transverse ridges.

Distribution: Mainland Asia, Malesia, Australia and one pantropical invasive (*E. urinaria*).

Notes —1. *Phyllanthus* subgenus *Emblica* was considered to have a disjunct distribution with four included sections, two from the Neotropics (*Microglochidion* and *Pityrocladus*) and two from the Palaeotropics (*Urinaria* and *Emblica*) (Webster 2002). In Bouman *et al.* (2021) it was shown that *Phyllanthus* subgenus *Emblica* was polyphyletic. The genus *Emblica* is here separated as a strictly Palaeotropical genus and the Neotropical sections are retained within *Phyllanthus* (as subgenus *Microglochidion* and subgenus *Phyllanthus* section *Pityrocladus*).

2. The genus *Emblica* is sister to a clade that contains the genera *Glochidion* (including *Phyllanthodendron* (Hemsl.) R.W.Bouman), *Breynia* (including *Sauropus*) and *Synsostemon*. The androecium may be similar to those found in the species of *Glochidion* subgenus *Phyllanthodendron*, but species in the groups differ in the shape of the disc glands in both types of flowers (ligulate glands in both flower types in subgenus *Phyllanthodendron*).

3. Staminate flowers within this genus are quite typical and usually have six sepals, six free orbicular disc glands and three stamens with connate filaments and vertically dehiscing anthers. However, some treatments are contradicting with six reported stamens, although this possibly refers to thecae (Chantaranothai 2007) or an entire disc (Chakrabarty & Balakrishnan 2018). These characters need to be verified as they contradict earlier descriptions (Hooker 1887; Beille 1927) without explanation. These characters have been tentatively included in the provided keys, but not in the above description.

4. We retain no further subdivision within the genus *Emblica* as the diagnostic characters of previously defined sections and subsections are minor. *Phyllanthus* section *Emblica* and section *Urinaria* differed mostly in habit (shrubs and trees vs. herbs), although woody shrubby plants from the Philippines were also placed in section *Urinaria*. *Emblica rufuschaneyi*, a shrubby species that would be placed in section *Emblica* is sister to a clade of herbaceous species and would result in a morphologically heterogeneous group if included. The staminate flowers in *Phyllanthus* sections *Emblica* and *Urinaria* are similar and we therefore opted to not retain any of the infrageneric groups. *Phyllanthus* subsection *Baeobotryoides*, which was created by Brunel (1987) to accommodate species with specialized inflorescence stalks, is also subsumed to avoid paraphyly. The genus has not been revised recently and species treatments have been scattered across several other

sections in older classifications of the genus *Phyllanthus*.
5. Rossignol *et al.* (1987) conducted a very thorough study of *E. urinaria* and several related species including morphology, Karyology and cross-breeding barriers. This resulted in a systematic revision which aimed to divide *Phyllanthus* section *Urinaria* into three subsections (subsection *Urinaria*, subsection *Arenarius* and subsection *Benguetensis*), but they only provided a full description for subsection *Urinaria*. Another of these subsections was planned to be published by Webster (2002 manuscript synopsis of subgenus *Phyllanthus*). Since these subsections delimit only a few species with very limited characters, these will not be pursued further.
6. Webster (1955) used the name of section *Urinaria*, based on the pre-Linnean work by Hermann (1717) and Burman (1737), but the name was validly published before as a subsection by Kuntze (1904) and placed in his section *Typhophyllanthus*. Therefore, the original author becomes Kuntze and not Webster as listed in Ralimanana & Hoffmann (2011) and Bouman *et al.* (2018).

Included species and taxonomic changes (45 spp.):

Emblica albizzioides (Kurz 1873: 239) R.W.Bouman, *comb. nov.* Basionym: *Cicca albizzioides* Kurz, homotypic synonym: *Phyllanthus albizzioides* (Kurz) Hooker (1887: 289).

Emblica anamalayanus (Gamble 1925: 330) R.W.Bouman, *comb. nov.* Basionym: *Pseudoglochidion anamalayanum* Gamble, homotypic synonym: *Phyllanthus anamalayanus* (Gamble) Webster (1994: 45).

Emblica andamanicus (Balakrisnan & Nair 1982 publ. 1983: 35) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus andamanicus* N.P.Balakr. & N.G.Nair. (non *Phyllanthus andamanicus* Kurz (1870: 47) pro syn. = *Glochidion helferi* (Müler 1865a: 372) Hook.f. (1887: 311)), homotypic synonym: *Phyllanthus balakrishnairii* Govaerts & Radcliffe-Smith (1996: 176).

Emblica angkorensis (Beille 1927: 583) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus angkorensis* Beille.

Emblica arenarius (Beille 1927: 587) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus arenarius* Beille.

Emblica baeobotryoides (Wallich ex Müller 1863: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus baeobotryoides* Wall. ex Müll.Arg.

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

Emblica bokorensis (Tagane 2015: 126) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus bokorensis* Tagane.

Emblica chamaepeuce (Ridley 1893: 345) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chamaepeuce* Ridl.

Emblica chayamaritiae (Chantaranothai & Kantachot *in* Kantachot & Chantaranothai 2013: 217) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus chayamaritiae* Chantar. & Kantachot.

Emblica coi (Wu, Ferreras & Chen 2017: 375) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus coi* M.J.Wu, Ferreras & Y.J.Chen.

Emblica collinsiae (Craib 1913: 72) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus collinsiae* Craib.

Emblica columnaris (Müller 1863: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus columnaris* Müll.Arg. (non *Phyllanthus columnaris* Warburg 1891: 356, nom. illeg.).

Emblica dealbatus (Alston 1931: 257) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dealbatus* Alston.

Emblica embergeri (Haicour & Rossignol *in* Rossignol *et al.* 1987: 1860) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus embergeri* Haicour & Rossignol.

Emblica erythrotrichus (Robinson 1911: 333) R.W.Bouman, comb. nov. Basionym: Phyllanthus erythrotrichus C.B.Rob.

Emblica geoffrayi (Beille 1927: 584) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus geoffrayi* Beille.

Emblica harmandii (Beille 1927: 586) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus harmandii* Beille.

Emblica multiflora (Hasskarl 1844: 240) R.W.Bouman, *comb. nov.* Basionym: *Agyneia multiflora* Hassk. (non *Phyllanthus multiflorus* Poiret (1804: 299), homotypic synonym: *Phyllanthus hasskarlianus* Müller (1863: 16).

Emblica fischeri Gamble (1925: 330) (non *Phyllanthus fischeri* Pax 1894: 77), homotypic synonym: *Phyllanthus indofischeri* Bennet *in* Raizada & Bennet (1983: 221).

Emblica kerrii (Airy Shaw 1969: 32) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kerrii* Airy Shaw.

Emblica lawii (Graham 1839: 181) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lawii* J.Graham.

Emblica marianus (Müller 1863: 17) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus marianus* Müll.Arg.

Emblica niinamii (Hayata 1904: 14) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus niinamii* Hayata.

Emblica officinalis Gaertner (1791: 122), homotypic synonym: *Phyllanthus emblica* Linnaeus (1753: 982), homotypic synonym: *Cicca emblica* (L.) Kurz (1877: 352).

Emblica oxyphyllus (Miquel 1861: 448) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus oxyphyllus* Miq. (non *Phyllanthus oxyphyllus* Müller, 1863: 40, nom. illeg.).

Emblica pachyphyllus (Müller 1866: 353) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pachyphyllus* Müll.Arg.

Emblica pacoensis (Thin 1992: 19) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus pacoensis* Thin.

Emblica pectinata (Hooker 1887: 290) Ridley (1924: 217), Basionym: *Phyllanthus pectinatus* Hook.f.

Emblica petelotii (Croizat 1942a: 30) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus petelotii* Croizat.

Emblica phuquocensis (Beille 1927: 581) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus phuquocensis* Beille.

Emblica prainianus (Collett & Hemsley 1890: 123) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus prainianus* Collett & Hemsl.

Emblica racemosa (Linnaeus f. 1782: 415) Sprengel (1826: 29), Basionym: *Phyllanthus racemosus* L.f., homotypic synonym: *Phyllanthus polyphyllus* Willdenow (1805: 586).

Emblica rheophyticus (Gilbert & Li 2008: 188) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rheophyticus* M.G.Gilbert & P.T.Li.

Emblica rufuschaneyi (van Welzen, Bouman & van der Ent *in* Bouman *et al.* 2018a: 4) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rufuschaneyi* Welzen, R.W.Bouman & Ent.

Emblica rupicola (Elmer 1910: 927) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rupicola* Elmer.

Emblica saffordii (Merrill 1914: 104) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus saffordii* Merr.

Emblica scabrifolius (Hooker 1887: 299) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus scabrifolius* Hook.f.

Emblica societatis (Müller 1866: 364) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus societatis* Müll.Arg.

Emblica submarginalis (Airy Shaw 1982: 33) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus submarginalis* Airy Shaw.

Emblica sulcatus (Hunter & Bruhl 1997b: 15) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sulcatus* J.T.Hunter & J.J.Bruhl.

Emblica thaii (Thin 1992: 22) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus thaii* Thin.

Emblica trungii (Thin 1992: 22) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus trungii* Thin.

Emblica tsarongensis (Smith 1921: 177) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus tsarongensis* W.W.Sm.

Emblica urinaria (Linnaeus 1753: 982) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus urinaria* L.

Clade H — Figs. 1, 2P, Q & R (Supplementary Fig. 1)

Glochidion J.R.Forst. & G.Forst.

Glochidion Forster & Forster (1776: t.57), nom. cons; Hooker (1887: 305); Beille (1927: 608); Airy Shaw (1972: 271); Whitmore (1973: 98); Webster (1994: 46); van Welzen (2000: 56); van Welzen *in* van Welzen *et al.* (2000: 81); Radcliffe-

Smith (2001: 47); van Welzen (2007: 308); Webster (2014: 79). — Type: *Glochidion ramiflorum* J.R.Forst & G.Forst.

Agyneia Linnaeus (1771: 161); Baillon (1858: 630). — Lectotype (designated by Webster 1994): *Agyneia pubera* L. = *Glochidion puberum* (L.) Müll.Arg.

Bradleia Banks ex Gaertner (1790: 127). — Type: *Bradleia sinica* Gaertn. = *Glochidion sinicum* (Gaertn.) Hook. & Arn.

Gynoon de Jussieu (1823: 335); (1824: 17). — Type: *Gynoon rigidum* A.Juss. = *Glochidion rigidum* (A.Juss.) Müll.Arg.

Glochidionopsis Blume (1826: 588); Baillon (1858: 639). — Type: *Glochidionopsis sericea* Blume = *Glochidion sericeum* (Blume) Hook.f.

Glochisandra Wight (1852: 26). — Type: *Glochisandra acuminata* Wight = *Glochidion lanceolarium* (Roxb.) Voigt.

Zarcoa Llanos (1857: 423). — Type: *Zarcoa philippica* Llanos = *Glochidion album* (Blanco) Boerl.

Glochidion J.R.Forst. & G.Forst. section *Hemiglochidion* Müller (1863: 58 61). — *Hemiglochidion* (Müll.Arg.) Schumann (1905: 289). — Lectotype (designated by Wheeler 1975): *Glochidion ramiflorum* J.R.Forst & G.Forst.

Phyllanthodendron Hemsley (1898: t. 2563, 2564). — *Phyllanthus* subgenus *Phyllanthodendron* (Hemsl.) Webster *in* Webster & Carpenter (2008: 608). — Type: *Phyllanthus mirabilis* Müll.Arg. (= formerly *Phyllanthodendron mirabile* (Müll.Arg.) Hemsl.) = *Glochidion mirabilis* (Müll.Arg.) R.W.Bouman.

Coccoglochidion Schumann (1905: 292). — Type: *Coccoglochidion erythrococcus* K.Schum. = *Glochidion philippicum* (Cav.) C.B.Rob.

Tetraglochidion Schumann (1905: 291). — Type: *Tetraglochidion gimi* K.Schum = *Glochidion gimi* (K.Schum.) Pax & K.Hoffm.

Diagnostic features: Shrubs (sometimes climbing) or trees, base sometimes succulent, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, sometimes differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base (not) auriculate. *Cataphylls* triangular. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, rarely paniculate. *Staminate flowers*: sepals 4–6; disc absent or sometimes segmented, 5 or 6, then usually alternating with sepals, ligulate; stamens 3–8, filaments connate, anthers elongate, erect, dehiscing vertically, connectives apiculate or not, when apiculate extensions tightly together (pyramidal), separating when flowers get older; pollen subprolate to prolate, 3–6-colporate, colpi monoporate, exine tectate to reticulate; pistillode absent (except in *G. moi* (P.T.Li) R.W.Bouman). *Pistillate flowers*: sepals 2–8, obovate to elliptic; disc absent or segmented, same number as sepals, alternating with sepals; ovary 3–15-locular; styles present or absent, usually connate in a slender or globular column; stigmas usually reduced, seldom free, subentire, bifid or usually completely fused in a cap-like structure. *Fruits* (inflated) capsules, sometimes with soft tissue. *Seeds* trigonous, woody or

fleshy, smooth or striate, with or without sarcotesta.
Distribution: Mainland Asia, Malesia, Australia, Pacific.
Note —Former *Phyllanthus* subgenus *Phyllanthodendron* is paraphyletic with the genus *Glochidion* nested within and is therefore synonymized with *Glochidion*. While the former subgenus *Phyllanthodendron* is morphologically distinguishable from *Glochidion*, by retaining it as a separate genus, *Phyllanthus* section *Pseudoactephila* Croizat would also need to be separated. When split this would result in two genera that are only distinguished based on inflorescence structure. Section *Pseudoactephila* is here transferred and raised to subgenus level to resolve the paraphyly of subgenus *Phyllanthodendron* and the previously defined sections are subsumed in the two subgenera. Not all sections have been included in a phylogenetic study so placement in either subgenus *Phyllanthodendron* or *Pseudoactephila* is here based on the presence or absence of specialized floriferous branchlets next to vegetative branchlets.

Glochidion J.R.Forst. & G.Forst. subgenus **Glochidion**

Glochidion J.R.Forst. & G.Forst. subgenus *Glochidion*: Literature and type as under the genus.

Diagnostic features: Shrubs or trees, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, not differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, unisexual or bisexual fascicles, rarely paniculate. *Staminate flowers*: sepals 5 or 6, spreading to recurving when old; disc absent; stamens 3–8, filaments connate, anthers erect, dehiscing vertically, connectives usually apiculate and apicula tightly together, sometimes broadened into a head; pollen suboblate to prolate, 3–6-colporate, exine reticulate to tectate; pistillode absent. *Pistillate flowers*: sepals 2–8; disc absent; ovary 3–15-locular; stigmas usually connate in a slender or globular column or cap-like structure, apex split into short stigmatic lobes, sometimes free and then stigmas bifid. *Fruits* capsules. *Seeds* trigonous, often with sarcotesta.
Distribution: Mainland Asia, Malesia, Australia, Pacific.
Notes —1. The combination of the genus *Glochidion* with *Phyllanthus* has been made several times in its history. As circumscribed here, subgenus *Glochidion* covers the traditional genus *Glochidion* excluding *Phyllanthodendron*. The relationship with subgenus *Phyllanthodendron* is remarkable as the flowers are very different: whereas the androecium consisting of connate stamens is similar, the absence of a floral disc in subgenus *Glochidion* is a notable distinction. Species of *Glochidion* are well known for their pollination system that involves mutualistic moths (Kato *et al.* 2003), but pollination observations in subgenus *Phyllanthodendron* are limited, with flies possibly implicated as potential pollinators (Kato & Kawakita 2017).

2. Several sections have been proposed for *Glochidion* by Müller (1865b, 1866), but the diagnostic characters, like the number of stamens, or locules in the ovary, overlap between sections. Within the genus (here subgenus) *Glochidion*, the following sections have been proposed: *Hemiglochidion* Müll.Arg., *Glochidiopsis* (Blume) Pax & K.Hoffm., *Scleroglochidion* (Müll.Arg.) Pax & K.Hoffm. and *Tetraglochidion* (K.Schum) Pax & K.Hoffm, but none are retained here. The species in subgenus *Glochidion* are usually difficult to distinguish and keys, where available, mostly rely on minute characters (van Welzen 2007).
3. Aside from morphological similarity between species that are usually quite variable, the phylogeny of *Glochidion* is poorly resolved (Luo *et al.* 2017). Reported branch lengths are often short or result in polytomies, suggesting that the diversification of *Glochidion* might have been a recent event and possibly enhanced by co-evolution with their mutualistic pollinators.

Included species and taxonomic changes: about 340 species, which are not all listed here. Transfers of *Glochidion* species to the genus *Phyllanthus* by Wagner & Lorence (2011) and Govaerts (2018) are reversed and treated below. The Indian species of subgenus *Glochidion* that were transferred to *Phyllanthus* by Chakrabarty & Balakrishnan (2009b), were reinstated following Chakrabarty & Balakrishnan (2018).
Glochidion acuminatissimum Airy Shaw (1972: 55), homotypic synonym: *Phyllanthus lalongatanus* Govaerts (2018: 95).
Glochidion acustylum Airy Shaw (1980b: 591), homotypic synonym: *Phyllanthus acustylus* (Airy Shaw) Govaerts (2018: 94).
Glochidion alstonii Airy Shaw (1981: 600), homotypic synonym: *Phyllanthus alstonii* (Airy Shaw) Govaerts (2018: 94).
Glochidion alticola Airy Shaw (1972: 8), homotypic synonym: *Phyllanthus alticola* (Airy Shaw) Govaerts (2018: 94).
Glochidion aluminescens Airy Shaw (1972: 16), homotypic synonym: *Phyllanthus aluminescens* (Airy Shaw) Govaerts (2018: 94).
Glochidion ambiguum Airy Shaw (1972: 62), homotypic synonym: *Phyllanthus ambiguus* (Airy Shaw) Govaerts (2018: 94).
Glochidion amentuligerum (Müller 1865a: 390) Croizat (1942b: 46). Basionym: *Phyllanthus amentuliger* Müll. Arg.
Glochidion andersonii Airy Shaw (1974: 287), homotypic synonym *Phyllanthus sarawakensis* Govaerts (2018: 95).
Glochidion anfractuosum Gibbs (1909: 168), homotypic synonym: *Phyllanthus anfractuosus* (Gibbs) Wagner & Lorence (2011: 69).
Glochidion angulatum Robinson (1909: 91), homotypic synonym: *Phyllanthus malesianus* Govaerts (2018: 95).
Glochidion apodogynum Airy Shaw (1972: 44), homotypic synonym: *Phyllanthus apodogynus* (Airy Shaw) Govaerts (2018: 94).

Glochidion atalotrichum Smith (1967: 74; homotypic synonym: *Phyllanthus atalotrichus* (A.C.Sm.) Wagner & Lorence (2011: 70).

Glochidion atrovirens Smith (1981: 481, 491), homotypic synonym: *Phyllanthus atrovirens* (A.C.Sm.) Wagner & Lorence (2011: 70).

Glochidion bracteatum Gillespie (1932: 15), homotypic synonym: *Phyllanthus bracteatus* (Gillespie) Wagner & Lorence (2011: 70).

Glochidion brothersonii Florence (1997a: 68), homotypic synonym: *Phyllanthus brothersonii* (J.Florence) Wagner & Lorence (2011: 70).

Glochidion brunnescens Smith (1981: 491), homotypic synonym: *Phyllanthus brunnescens* (A.C.Sm.) Wagner & Lorence (2011: 71).

Glochidion calciphilum Croizat (1942b: 46), homotypic synonym: *Phyllanthus calciphilus* (Croizat) Wagner & Lorence (2011: 71).

Glochidion christophersenii Croizat (1943a: 213), homotypic synonym: *Phyllanthus christophersenii* (Croizat) Wagner & Lorence (2011: 71).

Glochidion cleistanthoides Fosberg *in* Fosberg & Oliver (1991: 263), homotypic synonym: *Phyllanthus cleistanthoides* (Fosberg) Wagner & Lorence (2011: 71).

Glochidion comitum Florence (1997b: 29), homotypic synonym: *Phyllanthus comitus* (J.Florence) Wagner & Lorence (2011: 72).

Glochidion collinum Smith (1981: 494), homotypic synonym: *Phyllanthus vitilevuensis* Wagner & Lorence (2011: 90).

Glochidion concolor Müller (1863: 62), homotypic synonym: *Phyllanthus concolor* (Müll.Arg.) Müller (1865a: 374).

Glochidion cordatum Seemann ex Müller (1863: 64), homotypic synonym: *Phyllanthus cordatus* (Seem. ex Müll.Arg.) Müller (1865a: 376).

Glochidion cuspidatum (Müll.Arg.) Pax (1898: 645), homotypic synonym: *Phyllanthus cuspidatus* Müller (1865a: 377).

Glochidion emarginatum Moore (1933: 30), homotypic synonym: *Phyllanthus emarginatus* (J.W.Moore) Wagner & Lorence (2011: 73).

Glochidion euryoides Smith (1952: 373), homotypic synonym: *Phyllanthus euryoides* (A.C.Sm.) Wagner & Lorence (2011: 74).

Glochidion gillespiei Croizat (1942b: 46), homotypic synonym: *Phyllanthus gillespiei* (Croizat) Wagner & Lorence (2011: 74).

Glochidion gimi (Schumann 1905: 291); Pax & Hoffmann (1931: 58) Basionym: *Tetraglochidion gimi* K.Schum., homotypic synonym: *Phyllanthus gimi* (K.Schum.) Govaerts (2018: 94).

Glochidion grantii Florence (1996: 250), homotypic synonym: *Phyllanthus grantii* (J.Florence) Wagner & Lorence (2011: 74).

Glochidion grayanum (Müller 1865a: 380) Florence (1996: 253), homotypic synonym: *Phyllanthus grayanus* Müll.Arg.

Glochidion heterodoxum (Müller 1866: 321) Pax & Hoffmann (1931: 58), homotypic synonym: *Phyllanthus heterodoxus* Müll.Arg.

Glochidion hivaoaense Florence (1997a: 74), homotypic synonym: *Phyllanthus* *hivaoaensis* (J.Florence) Wagner & Lorence (2011: 74).

Glochidion hosokawae Fosberg *in* Fosberg & Oliver (1991: 261), homotypic synonym: *Phyllanthus hosokawae* (Fosberg) Wagner & Lorence (2011: 75).

Glochidion huahineense Florence (1997a: 75), homotypic synonym: *Phyllanthus huahineensis* (J.Florence) Wagner & Lorence (2011: 77).

Glochidion inusitatum Smith (1981: 493), homotypic synonym: *Phyllanthus inusitatus* (A.C.Sm.) Wagner & Lorence (2011: 77).

Glochidion kanehirae Hosokawa (1935: 22), homotypic synonym: *Phyllanthus* k*anehirae* (Hosok.) Wagner & Lorence (2011: 77).

Glochidion longfieldiae (Riley 1926: 55) Brown (1935: 141), homotypic synonym: *Phyllanthus longfieldiae* L.Riley.

Glochidion macrosepalum Hosokawa (1935: 21), homotypic synonym: *Phyllanthus macrosepalus* (Hosok.) Wagner & Lorence (2011: 78).

Glochidion manono Baillon ex Müller (1863: 65), homotypic synonym: *Phyllanthus manono* (Baill. ex Müll.Arg.) Müller (1865a: 377).

Glochidion marchionicum Brown (1935: 142), homotypic synonym: *Phyllanthus marchionicus* (F.Br.) Wagner & Lorence (2011: 79).

Glochidion marianum Müller (1863: 65), homotypic synonym: *Phyllanthus mariannensis* Wagner & Lorence (2011: 79), non *Phyllanthus marianus* Müller (1863: 17).

Glochidion melvilleorum Airy Shaw (1971: 487), homotypic synonym: *Phyllanthus melvilleorum* (Airy Shaw) Wagner & Lorence (2011: 81).

Glochidion multilobum Smith (1981: 493), homotypic synonym: *Phyllanthus multilobu*s (A.C.Sm.) Wagner & Lorence (2011: 81).

Glochidion nadeaudii Florence (1996: 253), homotypic synonym: *Phyllanthus nadeaudii* (J.Florence) Wagner & Lorence (2011: 81).

Glochidion orohenense Moore (1940: 6), homotypic synonym: *Phyllanthus orohenensis* (J.W.Moore) Wagner & Lorence (2011: 81).

Glochidion palauense Hosokawa (1935: 22), homotypic synonym: *Phyllanthus otobedii* Wagner & Lorence (2011: 81), non *Phyllanthus palauensis* Hosokawa (1935: 19).

Glochidion papenooense Florence (1996: 254), homotypic synonym: *Phyllanthus papenooensis* (J.Florence) Wagner & Lorence (2011: 83).

Glochidion pitcairnense (Brown 1935: 142) H.St.John in St. John & Philipson (1962: 187), Basionym: *Glochidion taitense* Baill. ex Müll.Arg. var. *pitcairnensis* F.Br., homotypic synonym: *Phyllanthus pitcairnensis* (F.Br.) Wagner & Lorence (2011: 83).

Glochidion podocarpum (Müller 1865a: 388) Robinson (1911: 330), homotypic synonym: *Phyllanthus podocarpus* Müll.Arg.

Glochidion ponapense Hosokawa (1935: 24), homotypic synonym: *Phyllanthus ponapensis* (Hosok.) Wagner & Lorence (2011: 84).

Glochidion moorei Li (1982: 117), homotypic synonym: *Phyllanthus raiateaensis*

Wagner & Lorence (2011: 84).

Glochidion raivavense Brown (1935: 142), homotypic synonym: *Phyllanthus raivavensis* (F.Br.) Wagner & Lorence (2011: 85).

Glochidion rapaense Florence (1996: 258), homotypic synonym: *Phyllanthus rapaensis* (J.Florence) Wagner & Lorence (2011: 85).

Glochidion myrtifolium Moore (1963: 10), homotypic synonym: *Phyllanthus st-johnii* Wagner & Lorence (2011: 86).

Glochidion samoanus (Müller (1866: 289) R.W.Bouman, *comb. nov.*, *stat. nov.* Basionym: *Phyllanthus ramiflorus* (J.R.Forst. & G.Forst.) Müll.Arg. var. *samoanus* Müll.Arg., homotypic synonym: *Phyllanthus samoanus* (Müll.Arg.) Wagner & Lorence (2011: 86).

Glochidion seemannii Müller (1863: 63), homotypic synonym: *Phyllanthus seemannii* (Müll.Arg.) Müller (1865a: 374).

Glochidion senyavinianum Glassman (1952: 71), homotypic synonym: *Phyllanthus senyavinianus* (Glassman) Wagner & Lorence (2011: 87).

Glochidion sessilis (Warburg 1891: 357) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus sessilis* Warb.

Glochidion taitense Baillon ex Müller (1863: 66), homotypic synonym: *Phyllanthus taitensis* (Baill. ex Müll.Arg.) Müller (1865a: 380).

Glochidion temehaniense Moore (1963: 15), homotypic synonym: *Phyllanthus temehaniensis* (J.W.Moore) Wagner & Lorence (2011: 88).

Glochidion tuamotuense Florence (1997a: 98), homotypic synonym: *Phyllanthus tuamotuensis* (J.Florence) Wagner & Lorence (2011: 89).

Glochidion vitiense (Müller 1865a: 374) Gillespie (1932: 17), homotypic synonym: *Phyllanthus vitiensis* Müll.Arg.

Glochidion websteri Fosberg *in* Fosberg & Oliver (1991: 262), homotypic synonym: *Phyllanthus websteri* (Fosberg) Wagner & Lorence (2011: 90).

Glochidion wilderi Florence (1997a: 99), homotypic synonym: *Phyllanthus wilderi* (J.Florence) Wagner & Lorence (2011: 90).

Glochidion J.R.Forst. & G.Forst. subgenus **Phyllanthodendron** (Hemsl.) R.W.Bouman, *comb. nov*.

Phyllanthodendron Hemsley (1898: t. 2563); Ridley (1924: 205); Croizat (1942a: 33); Li (1987b: 8). — *Phyllanthus* L. section *Phyllanthodendron* (Hemsl.) Beille (1925: 160); Pax & Hoffmann (1931: 63). — *Phyllanthus* L. subgenus *Phyllanthodendron* (Hemsl.) Webster (2008: 608). — Type: *Phyllanthodendron mirabile* (Müll.Arg.) Hemsl. (formerly *Phyllanthus mirabilis* Müll.Arg.) = *Glochidion mirabilis* (Müll. Arg.) R.W.Bouman.

Phyllanthodendron Hemsl. section *Euphyllanthodendron* Croizat (1942a: 33), *nom. inval.* — Type: *Phyllanthus mirabilis* Müll.Arg.(see Airy Shaw (1960: 469) and note 2) = *Glochidion lingulatum* (Beille) R.W.Bouman.

Phyllanthodendron Hemsl. section *Calophyllum* Croizat (1942a: 33). — Type: *Phyllanthus anthopotanicum* Hand.-Mazz (formerly *Phyllanthodendron anthopotamicum* (Hand.-Mazz.) Croizat) = *Glochidion anthopotanicum* (Hand.-Mazz) R.W.Bouman.

Diagnostic features: Shrubs (sometimes climbing) or trees, base sometimes succulent, monoecious or dioecious, branching phyllanthoid, branchlets pinnatiform, differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, bisexual fascicles. *Staminate flowers*: sepals 5 or 6; disc glands 5 or 6, free, ligulate; stamens 3 (or 4), filaments connate, anthers erect, dehiscing vertically, connectives usually apiculate; pollen subprolate, 4-colporate, colpi monoporate, exine reticulate; pistillode absent. *Pistillate flowers*: sepals 5 or 6, oblong, obovate-elliptic; disc glands 5 or 6, free, ligulate; ovary 3-locular; styles present or absent; stigmas bifid or subentire. *Fruits* (inflated) capsules. *Seeds* trigonous, striate, hollow ventrally.
Distribution: Mainland Asia.
Notes —1. *Phyllanthodendron* Hemsl. was a separate genus that was retained in the Flora of China (Li 1987b), while other treatments include it as a section within *Phyllanthus* (see treatment of species in Beille 1925; Chantaranothai 2007). Several sections have been defined, often based on the habit or number of sepals and stamens, but the differences are often small. These sections are here subsumed, with *Phyllanthus* sections *Phyllanthodendron* and *Calophyllum* placed in subgenus *Phyllanthodendron* on account of the specialized floriferous branchlets. Sections *Tetrandrum*, *Pseudoactephila* and *Arachnodes* do not have floriferous branchlets and are subsumed in subgenus *Pseudoactephila*.
2. Croizat (1942a) divided the genus *Phyllanthodendron* Hemsl. in three sections, section *Phyllanthodendron*, *Pseudoactephila* and *Calophyllum* Croizat. *Phyllanthus lingulatus* Beille was incorrectly designated as the type of section *Phyllanthodendron* (type of the genus Phyllanthodendron is *P. mirabilis* (Müll.Arg.) Hemsl.), which was later corrected by Airy Shaw (1960).

Included species and taxonomic changes (5 spp.):
Glochidion anthopotamicus (Handel-Mazzetti 1931: 223) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus anthopotamicus* Hand.-Mazz.
Glochidion dongmoensis (Thin 1992: 16) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus dongmoensis* Thin.
Glochidion dunnianus (Léveillé 1911: 324) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron dunnianum* H.Lév., homotypic synonym: *Phyllanthus dunnianus* (H.Lév.) Hand.-Mazz. ex Rehder (1933: 230).
Glochidion kaweesakii (Pornpongrungrueng, Chantaranothai & Parnell *in* Pornpongrungrueng *et al.* 2017: 572) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus kaweesakii* Pornp., Chantar. & J.Parn.

Glochidion mirabilis (Müller 1864: 513) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus mirabilis* Müll.Arg.

Glochidion J.R.Forst. & G.Forst. subgenus **Pseudoactephila** (Croizat) R.W.Bouman, *stat. et comb. nov.*

Phyllanthus L. subgenus *Phyllanthodendron* (Hemsl.) G.L.Webster section *Pseudoactephila* Croizat (1942a: 33). — Type: *Phyllanthus roseus* (Craib & Hutch.) Beille (= *Phyllanthodendron roseum* Craib & Hutch. = *Glochidion roseum* (Craib & Hutch.) R.W.Bouman).
Uranthera Pax & Hoffmann (1911: 95), *nom. illeg.*, non *Uranthera* Naudin (1845: 189). — Type: *Uranthera siamensis* Pax & K.Hoffm. (= formerly Phyllanthus roseus (Craib & Hutch.) Beille) = *Glochidion roseum* (Craib & Hutch.) R.W.Bouman.
Arachnodes Gagnepain (1950: 32). — *Phyllanthus* L. subgenus *Phyllanthodendron* (Hemsl.) G.L.Webster section *Arachnodes* (Gagnep.) Airy Shaw (1960: 470). — Type: *Arachnodes chevalieri* Gagnep. (non *Glochidion chevalieri* Beille 1927: 615) (= formerly *Phyllanthus arachnodes* Govaerts & Radcl.-Sm.) = *Glochidion arachnodes* (Govaerts & Radcl.-Sm.) R.W.Bouman.
Phyllanthodendron Hemsl. section *Tetrandrum* Li (1987b: 8). — Type: *Phyllanthodendron moi* (P.T.Li) P.T.Li (= formerly *Phyllanthus moi* P.T.Li) = *Glochidion moi* (P.T.Li) R.W.Bouman.

Diagnostic features: Shrubs, sometimes twining, monoecious, branching phyllanthoid, branchlets pinnatiform, not differentiated in vegetative and floriferous branchlets. *Brachyblasts* absent. *Leaves* distichous. *Inflorescences* axillary, bisexual, flowers crowded in long-pedicelled clustered fascicles. *Staminate flowers*: sepals 4–6; disc glands 4–6, free, ligulate; stamens 3 or 4, filaments connate, anthers erect, dehiscing vertically, connectives usually apiculate; pollen subprolate, 4-colporate, colpi monoporate, exine reticulate; pistillode absent (except in *G. moi*). *Pistillate flowers*: sepals 5 or 6; disc glands 5 or 6, free, ligulate; ovary 3-locular; styles?; stigmas bifid to entire. *Fruits* (inflated) capsules. *Seeds* trigonous.
Distribution: Mainland Asia.
Note —Phyllanthodendron section *Tetrandrum* was a monotypic section for a species with a 4-merous staminate flower that is here subsumed as the number of sepals is considered variable within the subgenus. *Phyllanthodendron* section *Arachnodes* was mainly distinguished by its twining habit.

Included species and taxonomic changes (14 spp.):
Glochidion arachnodes (Govaerts & Radcliffe-Smith 1996: 175) R.W.Bouman, *comb. nov.* Basionym: *Arachnodes chevalieri* Gagnepain (1950: 32, non *Glochidion chevalieri* Beille 1927: 615), homotypic synonym: *Phyllanthus*

arachnodes Govaerts & Radcl.-Sm.

Glochidion breyniopsis Esser & R.W.Bouman, *nom. nov.* (non *G. breynioides* Robinson 1909: 95), Basionym: *Phyllanthodendron breynioides* P.T.Li (1987b: 6), homotypic synonym: *Phyllanthus breynioides* (P.T.Li) Govaerts & Radcliffe-Smith (1996: 176).

Glochidion carinatum (Beille 1925: 160) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus carinatus* Beille, homotypic synonym: *Phyllanthodendron carinatum* (Beille) Croizat (1942a: 36).

Glochidion caudatifolium (Li 1987b: 7) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron caudatifolium* P.T.Li, homotypic synonym: *Phyllanthus lii* Govaerts & Radcliffe-Smith (1996: 177).

Glochidion lativenium (Croizat 1942a: 36) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron lativenium* Croizat, homotypic synonym: *Phyllanthus lativenius* (Croizat) Govaerts & Radcliffe-Smith (1996: 177).

Glochidion lingulatum (Beille 1925: 161) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus lingulatus* Beille.

Glochidion moi (Li 1983: 167) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus moi* P.T.Li.

Glochidion orbicularifolium (Li 1987b: 5) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron orbicularifolium* P.T.Li, homotypic synonym: *Phyllanthus orbicularifolius* (P.T.Li) Govaerts & Radcliffe-Smith (1996: 177).

Glochidion petraeum (Li 1987b: 4) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron petraeum* P.T.Li, homotypic synonym: *Phyllanthus guanxiensis* Govaerts & Radcliffe-Smith (1996: 176).

Glochidion poilanei (Beille 1925: 162) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus poilanei* Beille.

Glochidion minutiflorum (Ridley 1911: 169) R.W.Bouman, *comb. nov.* Basionym: *Cleistanthus minutiflorus* Ridl., homotypic synonym: *Phyllanthus ridleyanus* Airy Shaw (1972: 323).

Glochidion roseum (Craib & Hutchinson 1910: 23) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron roseum* Craib & Hutch., homotypic synonym: *Phyllanthus roseus* (Craib & Hutch.) Beille (1927: 590).

Glochidion rubicundum (Beille 1925: 162) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthus rubicundus* Beille.

Glochidion yunnanense (Croizat 1942a: 36) R.W.Bouman, *comb. nov.* Basionym: *Phyllanthodendron yunnanense* Croizat, homotypic synonym *Phyllanthus yunnanensis* (Croizat) Govaerts & Radcliffe-Smith (1996: 178).

Clade I — Fig. 1, 2N & O (supplementary fig. 1)

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

Breynia Forster & Forster (1776: 145), nom. cons.— Type: *Breynia disticha* J.R.Forst.

& G.Forst. (for a more expanded nomenclature of *Breynia* and its subgeneric groups, see van Welzen *et al.* 2014a).

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Cataphyllary stipules* triangular, indurate, base not auriculate. *Cataphylls* triangular to elongate. *Leaves* distichous. *Inflorescences* axillary, usually unisexual fascicles, sometimes larger compound inflorescences. *Staminate flowers* discoid or campanulate to turbinate; sepals 6, usually connate for half to whole length with some exceptions, with sepal scales (absent in *B. granulosa* (Airy Shaw) Welzen & Pruesapan, *B. kerrii* (Airy Shaw) Welzen & Pruesapan, *B. pierrei* (Beille) Welzen & Pruesapan, *B. pulchella* (Airy Shaw) Welzen & Pruesapan, *B. shawii* (Welzen) Welzen & Pruesapan, *B. subterblanca* (C.E.C.Fisch.) C.E.C.Fisch., and *B. rostrata* Merr.); disc absent; stamens 3, filaments connate, free parts horizontal or oblique or fused and vertical; anthers dehiscing lengthwise (same as vertically in other genera); pollen 4–16-colporate, colpi diploporate, exine (micro) reticulate, tectate; pistillode absent. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular, sometimes with an apical rim; styles absent; stigmas bifid or entire, horizontal to erect, sometimes reduced. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.
Distribution: Mainland Asia (to China), Malesia, Australia, Pacific.
Note —Mainly distinguished from the genus *Synostemon* by the subglobose ovaries that are usually flattened apically, bifid stigmas that are usually split for more than half of their length and smooth seeds (van Welzen *et al.* 2014a). 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.* 2014a).

Breynia J.R.Forst. & G.Forst. subgenus **Breynia**

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

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Inflorescences* axillary, usually unisexual fascicles. *Staminate flowers* discoid or campanulate to turbinate; sepals 6, connate for half to almost completely; disc absent; stamens 3, filaments connate, connective also sometimes fused; anthers dehiscing vertically; pollen 4–12-colporate, colpi diploporate, exine (micro-) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular, sometimes with an apical rim; styles absent; stigmas bifid or entire, horizontal to erect, sometimes reduced in size. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.
Distribution: Mainland Asia, Malesia, Australia, Pacific.

Breynia J.R.Forst. & G.Forst. section **Breynia**

Breynia J.R.Forst. & G.Forst. section *Breynia*: Literature and type as under the genus.
Breynia section *Breyniastrum* Baillon (1866: 344). — Lectotype (designated by Esser *in* van Welzen *et al.* 2014a): *Breynia stipitata* Müll.Arg.

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Staminate flowers*: campanulate to turbinate; sepals 6, usually connate for whole length; disc absent; stamens 3, filaments connate, connective also sometimes fused; anthers dehiscing vertically; pollen 4–12-colporate, colpi diploporate, exine (micro) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular; styles absent; stigmas bifid or entire, horizontal to erect, often reduced in size. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.
Distribution: Mainland Asia, Malesia, Australia, Pacific.

Breynia J.R.Forst. & G.Forst. section **Cryptogynium** (Müll.Arg.) Welzen & Pruesapan

Breynia J.R.Forst. & G.Forst. section *Cryptogynium* (Müll.Arg.) Welzen & Pruesapan *in* van Welzen *et al.* (2014: 89); van Welzen (2017: 90). —Type: *Ceratogynum rhamnoides* Wight = *Breynia quadrangularis* (J.G.Klein ex Willd.) Chakrab. & N.P.Balakr.

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Staminate flowers* discoid; sepals 6, usually connate for half to whole length with some exceptions; disc absent; stamens 3, filaments connate, connective also sometimes fused, anthers dehiscing horizontally to vertically; pollen 6–12-colporate, colpi diploporate, exine (micro) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular, sometimes with an apical rim; styles absent; stigmas bifid, horizontal to erect. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.
Distribution: Mainland Asia, Malesia.

Breynia J.R.Forst. & G.Forst. subgenus **Sauropus** (Blume) Welzen & Pruesapan

Breynia J.R.Forst. & G.Forst. subgenus *Sauropus* (Blume) Welzen & Pruesapan in van Welzen *et al.* (2014: 91). — Type: *Sauropus stipitatus* Hook.f. = *Breynia gynophora* Welzen & Pruesapan.

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid, branchlets pinnatiform. *Brachyblasts* absent. *Inflorescences* axillary, usually unisexual fascicles, sometimes larger and longer compound inflorescences. *Staminate flowers* discoid; sepals 6, usually connate for half to completely with some exceptions; disc absent; stamens 3, filaments connate, connectives horizontal, with thecae hanging underneath, dehiscing vertically; pollen 8-16-colporate, colpi diploporate, exine (micro) reticulate, tectate. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular; styles absent; stigmas bifid, horizontal to ascending. *Fruits* capsules, tardily dehiscent, wider than long. *Seeds* trigonous, smooth.
Distribution: Mainland Asia, Malesia, Australia.
Note — Other characters that might be useful for distinguishing this group from other *Breynia* species include the considerably large leaf size in most species, with the exception of *B. carnosa* Welzen & Pruesapan (Van Welzen *et al.* 2014a).

Synostemon F.Muell.

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

Diagnostic features: Shrubs or herbs, monoecious, branching phyllanthoid or subphyllanthoid, branchlets pinnatiform. *Brachyblasts* absent (except in *S. rigens* F.Muell.). *Cataphyllary stipules* triangular, indurate or membranous, base not auriculate. *Cataphylls* triangular to elongate. *Inflorescences* axillary, usually unisexual fascicles. *Staminate flowers*: campanulate to turbinate; sepals 6, connate or free, without sepal scales (except present in *S. bacciformis* (L.) G.L.Webster and *S. anemoniflorus* (J.T.Hunter & J.J.Bruhl) I.Telford & Pruesapan); disc absent; stamens 3, filaments connate, connectives often fused, apiculate with apicula free or fused in a cap; anthers dehiscing vertically; pollen 3–8-colporate, colpi diploporate, exine (micro) reticulate, heterobrochate; pistillode absent. *Pistillate flowers*: sepals 6; disc absent; ovary 3-locular, sometimes with a (slight) rim; styles absent; stigmas bifid (except in *S. elachophyllus* (F.Muell.) Airy Shaw), erect or spreading. *Fruits* capsules, schizocarpic, subglobose or ovoid, longer than wide. *Seeds* trigonous, prominently sculptured.
Distribution: Mainly Australia with one species also occurring in Malesia (*Synostemon sphenophyllus* Airy Shaw in Papua New Guinea) and one widespread tropical coastal Indian and western Pacific Ocean species, *S. bacciformis*.
Notes — *Synostemon* has recently been enlarged through close taxonomic study (Telford & Naaykens 2015; Telford *et al.* 2015, 2016, 2019) and consists of about 41 species (one unpublished). Only species that were still not transferred are listed below.

Included species and taxonomic changes: Five previously untreated species of

Sauropus are transferred here to *Synostemon* to complete the reinstatement of *Synostemon*.

Synostemon anemoniflorus (Hunter & Bruhl 1997a: 662) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus anemoniflorus* J.T.Hunter & J.J.Bruhl.

Synostemon arenosus (Hunter & Bruhl 1997b: 166) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus arenosus* J.T.Hunter & J.J.Bruhl.

Synostemon brunonis (Moore 1920: 213) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus brunonis* (S.Moore) Airy Shaw (1980c: 672).

Synostemon huntii (Ewart & Davies 1917: 164) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus huntii* (Ewart & O.B.Davies) Airy Shaw (1980c: 679).

Synostemon paucifolius (Hunter & Bruhl 1997b: 172) I.Telford & J.J.Bruhl, *comb. nov.* Basionym: *Sauropus paucifolius* J.T.Hunter & J.J.Bruhl.

Doubtful species

Phyllanthus petiolaris Roxb. was described by Roxburgh (1832), but he only mentioned the habit and the presence of flowers. More details on the flowers are necessary to place it in any genus. Based on its location, the species could be in any of these genera: *Cathetus*, *Nymphanthus* or *Emblica*. Balakrishnan & Chakrabarty (2007) treat this as an unplaced name.

Discussion & conclusions

This treatment is a proposed solution to the paraphyly of the genus *Phyllanthus*. By reinstating nine other genera separated from *Phyllanthus* along with other subgeneric realignments we feel confident that this classification is a much better reflection of the evolutionary history of this group. All genera proposed here are monophyletic in our phylogenetic analyses (Suppl Fig.1; Bouman *et al.* 2021) and might be used for further extensive studies. Many genera have not received a full taxonomic treatment as a group, and future revisions could result in the recognition of new species. Some of relationships found in Bouman *et al.* (2021) were surprising and in contrast with morphology based classification as the morphological character states used are of parallel origin. These are interesting for further study (such as the relation between groups within the genus *Glochidion*).

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).

Appendix 8-1. Species specific differences with previous classification by Bouman *et al.* (2018: table 2).

Several species were treated in the main text in other subgeneric groups differing from the species table presented by Bouman *et al.* (2018b). In this appendix we briefly explain minor changes and species transfers that are not treated in the main text, but were the result of new information.

Australian species of *Dendrophyllanthus*

Three Australian species here treated in the genus *Cicca* (*C. lacunella*, *C. lacunaria* and *C. erwinii*) were originally placed in *Phyllanthus* section *Antipodanthus* or *Lysiandra*, but were found to be nested in the clade of *Dendrophyllanthus* (supplementary fig. 1).

Species by Blanco (1837, 1845)

Two species described by Blanco (1845) were brought to our attention by P. Pelser (pers. comm.) while discussing identifications for Co's Digital Flora of the Philippines (Pelser *et al.*, 2011 onwards). At the time we had seen no material of these species and they were treated by Müller (1866) in a section that seemed to be synonymized under the genus *Flueggea* Barker & Welzen 2010). However, this was a consequence of a wrong identification of the type material of *P. glaucus*, which was corrected in Chakrabarty & Balakrishnan (2018). The two following species were originally published in the genus *Kirganelia* and seemed valid, but were reduced to synonymy by Merrill (1918), which is followed here until more material is collected. This means that we still treat both names as synonyms and do not include them in the genus *Kirganelia*. Merrill (1918) synonymized *P. nigrescens* (Blanco) Müll.Arg. under *Glochidion lancifolium* and *P. pumilus* (Blanco) Müll.Arg. as *P. niruri* (though *P. amarus* or *P. debilis*, here *M. amara* and *M. debilis* are more likely).

Species by Koorders

The affinities of *P. celebicus* Koord. and *P. minahassae* Koord. were not known during the study of Bouman *et al.* (2018b). Subsequent study of the type material showed these species to have the characteristic flowers of species in *Phyllanthus* subgenus *Eriococcus* (Bouman *et al.* 2019), which are all transferred here to the reinstated genus *Nymphanthus*.

Indian species of *Phyllanthus* s.l.

The subgeneric placements in Chakrabarty & Balakrishnan (2018) mostly follow Webster (1956, 1957, 1958), but later modifications proposed by Brunel (1987) or Ralimanana & Hoffmann (2011, 2013) are not incorporated. Phyllanthoid branching, which is a phylogenetically informative character, is mentioned in the descriptions of several groups, but not applied consistently. Without the inclusion of pictures of the flowers and specimens with clear depiction of the branching system, many placements here await inclusion of a palynological or phylogenetic study.

Phyllanthus ajmerianus L.B.Chaudhary & R.R.Rao (here *Moeroris ajmerianus* (L.B.Chaudhary & R.R.Rao) R.W.Bouman) is treated here in *Moeroris* subgenus *Tenellanthus* on account of its 5-merous staminate flower with 5 stamens that are partially connate at the base (see Chaduhary & Rao 2006). The longitudinally striate seed is also common in the genus *Moeroris* and subgenus *Tenellanthus* contains more cryptophytic species.

Phyllanthus brevipes Hook.f. was treated in *Phyllanthus* subgenus *Afroswartziani* (Bouman *et al.* 2018b), but is probably a species of *Cathetus* subgenus *Macraea*. Chakrabarty & Balakrishnan (2018) treat this species in *Phyllanthus* subgenus *Phyllanthus*, but mention that laminate leaves are present on all axes (non-phyllanthoid branching?) and it is therefore treated here in the genus *Cathetus*. The staminate flower has 3 partially connate stamens and the pistillate disc is 6 lobed, but not segmented which is more typical for *Cathetus* subgenus *Macraea* than the genus *Nellica*.

Phyllanthus griffithii Müll.Arg. was listed in Bouman *et al.* (2018b), but *P. stylosus* Griff. was published earlier and is a valid epithet. *Phyllanthus griffithii* is therefore listed here as a synonym of *P. stylosus* following treatments that consider this to be the same species (Chakrabarty & Balakrishnan 2018). Specimens attributed to *P. stylosus* bear leaves on all axes (specimen W. Griffith 4822 deposited at K with barcodes K000246565, K000246566), only basally connate stamens and an entire pistillate disc (Chakrabarty & Balakrishnan 2018). It is treated here in *Cathetus* subgenus *Macraea*.

Phyllanthus hakgalensis Thwaites ex Trimen was tentatively placed by Webster (1997) in section *Paraphyllantus* (now genus *Nellica*), but he mentioned that this species has an entire pistillate disc, which is more typical for *Cathetus* subgenus *Macraea*. Based on the entire pistillate disc and three free stamens in the staminate flower, it is here treated in *Cathetus* subgenus *Macraea*. Verwijs *et al.* (2019) did not include this species in their treatment of subgenus *Macraea*, but did discuss similarities. Chakrabarty & Balakrishnan (2018) treated this species in *Phyllanthus* subgenus *Eriococcus* (now genus *Nymphanthus*) based on descriptions by Alston (1931), which would need to be confirmed. Unfortunately, this species is only known from the type specimen. Webster (1997) described the phyllotaxis as spiral, which could be plesiomorphic or this species might be related to *Cicca* subgenus *Betsileani* (Jean F.Brunel) Ralim. & Petra Hoffm. (very unlikely considering its geographical range). Perhaps the pollen could be informative, but this species has not been included in any previous palynological study.

Phyllanthus leschenaultii Müll.Arg. has phyllanthoid branching and is described as having partially connate filaments in the staminate flower with horizontally dehiscing orbicular anthers (Chakrabarty & Balakrishnan 2018). This is comparable to *Moeroris* subgenus *Moeroris*. However, we could not confidently confirm the branching type and, less likely, it could also be a species of *Cathetus* subgenus *Macraea*.

Phyllanthus mozambicensis Gand. was still listed as an accepted species in Govaerts *et al.* (2000) and Bouman *et al.* (2018b), but Radcliffe-Smith (1996) treats it as a synonym of *P. parvulus*. As this epithet has to our knowledge not been reinstated as a separate species, it is only treated as a synonym here and not separately transferred to the genus *Moeroris*.

Phyllanthus parvifolius Buch.-Ham. ex D.Don is treated similarly to *P. stylosus* and *P. praetervisus* and placed in *Cathetus* subgenus *Macraea* (see Mitra & Sanjappa 2003 for more information on these complex species). The difficulty in assigning these species also lies in the apparent fusion of the filaments, which can be variable in species of *Cathetus* subgenus *Macraea*. A palynological study by Sagun & Van der Ham (2003) mentions unpublished data from Punt gouping the pollen of *P. griffithii* (here *C. stylosus*), *P. parvifolius* and *P. praetervisus* in one type that approaches pantoporate pollen (as seen in *Cathetus* subgenus *Cathetus*).

Phyllanthus pseudoparvifolius R.L.Mitra & Sanjappa is treated in the genus *Cathetus*. The free stamens in the staminate flower and ornamentation of the seeds are similar to other species of *Cathetus* subgenus *Macraea*, and it is therefore included here. Unfortunately, this placement is also tentative and awaits a palynological or phylogenetic study.

The syntypes of *Phyllanthus praetervisus* Müll.Arg. in BR seem to be a mixture. One appears to have non-phyllanthoid branching with leaves on all axes (BR0000013336042) and the other has phyllanthoid branching with fascicled branchlets (BR0000005100972). *Phyllanthus praetervisus* is tentatively placed in *Cathetus* subgenus *Macraea*, but the material listed in Chakrabarty & Balakrishnan (2018) as isotypes do not appear to be from the same collection.

Phyllanthus pendulus Roxb. is placed in the genus *Moeroris*, but there are only some meagre literature descriptions available (see Chakrabarty & Balakrishnan 2007, 2018).

Individual cases (treated alphabetically)

Phyllanthus caesius Airy Shaw & G.L.Webster was originally placed by Airy Shaw & Webster (1971) in subgenus *Kirganelia*, but later treated in subgenus *Gomphidium* (Airy Shaw 1980). After reviewing the isotype stored at L (L0016415), we decided to follow the latter placement in subgenus *Gomphidium* (here in genus *Dendrophyllanthus*).

Phyllanthus caudatifolius Merr. was placed in subgenus *Kirganelia* with some doubt and after seeing the type specimen *R.C. McGregor 43867* from K (K001056679) and dissecting a flower, it seems better placed in what we consider *Dendrophyllanthus* section *Leptonema*.

Phyllanthus dumetosus Poir. was treated in subgenus *Kirganelia* and listed as occurring in the Philippines, but this was a mistake in the JSTOR's Global Plants database (https://plants.jstor.org/). After studying material of this species from K, we treat it in the genus *Moeroris* subgenus *Tenellanthus*.

Phyllanthus fallax Müll.Arg. is treated in *Phyllanthus* section *Loxopodium* since the type seems to have non-phyllanthoid branching.

Phyllanthus lasiogynus Müll.Arg. is not further placed in any subgenus, but appears to have phyllanthoid branching and is probably better suited to stay in the genus *Phyllanthus*.

Phyllanthus lunifolius Gilbert & Thulin is doubtfully treated in the genus *Moeroris*, mainly because of its distribution. Staminate flowers are needed to confirm placement. It has large brachyblasts, but these also occur in the genus *Cicca*. Its ericoid leaves are unusual within the African species of *Phyllanthus* and its relation to other species is unknown.

Phyllanthus polyphyllus Willd. is treated as synonym of *Emblica racemosus* following Chakrabarty & Balakrishnan (2017 as *Phyllanthus racemosus*).

Phyllanthus pseudocarunculatus Radcl.-Sm. is a later homotypic synonym of Brunel's (1987) *P. carunculatus*. Both names are based for the same material and Radcliffe-Smith (1996) published his later name under the assumption that Brunel´s name (1987) was not validly published.

Phyllanthus rupicola Elmer is treated in the genus *Emblica* since it bears great similarity to *E. erythrotrichus*. However, the staminate flower was never described and is needed to confirm this placement.

Phyllanthus securinegoides Merr. could also be *Emblica* based on pollen described in Wu *et al.* 2016. The same is true for *P. glochidioides* which has no description of the staminate flower. The Philippine *P. apiculatus* should also be checked to determine whether it belongs in the genus *Dendrophyllanthus* (here done provisionally) or in the genus *Emblica*.

Phyllanthus squamifolius (Lour.) Stokes and *P. villosus* (Lour.) Müll.Arg. were also treated in *Nymphanthus* on account of their geography and because they were originally also treated in that genus. No material was seen of these species and more collections are needed to confirm our placement.

Phyllanthus triphlebius C.B.Rob. is treated in the genus *Nymphanthus*, but its pollen is very different from the other species of this genus (see Wu *et al.* 2016).

Phyllanthus udoricola Radclf.-Sm. was described by Radcliffe-Smith (1996b) 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 8-2. Shown on following pages.

Supplementary figure 8-1. Phylogeny of tribe Phyllantheae from combined dataset of Bouman *et al.* (2021) and Falcón *et al.* (2020) showing the new classification proposed here; clade labels A-I follow figure 1. Dataset is composed of nuclear (ITS and *PHYC*) and plastid (*accD–psaI*, *matK* and *trnS–trnG*) markers. Posterior probabilities (PP) from Bayesian inference are displayed above nodes; Maximum Likelihood bootstrap scores are displayed below the nodes. Undescribed species are indicated with an asterisk (*).
https://www.biotaxa.org/Phytotaxa/article/view/phytotaxa.540.1.1/71295

Appendix 8-2. GenBank accessions numbers used in phylogenetic analyses. The majority of sequences came from Kathriarachchi *et al.* (2006), Pruesapan *et al.* (2008, 2012), Kawakita & Kato (2009), Falcón *et al.* (2020) and Bouman *et al.* (2021). GenBank accessions from Falcón *et al.* (2020) are highlighted in bold.

Matrix name	**Voucher**	**ITS**	**PHYC**	***accD-psaI***	***matK***	***trnS-trnG***
Actephila excelsa	Bouman & Yong RWB057 (HITBC)		MN904188	MN915296	MN916079	
Antidesma bunius	Gent living collection xx0Gent19002015		MN904189		MN916080	
Breynia amoebiflora	Maxwell 90-721 (L)				EU643747	
Breynia amoebiflora	Kerr 19655 (P)	GQ503379	GQ503437	GQ503498		GQ503562
Breynia androgyna (1)	Van Welzen 2006-4 (L)	EU623563	GQ503439	GQ503500	EU643748	GQ503564
Breynia androgyna (3)	Kathriarachchi et al. 40 (K)	AY936747	GQ503459	GQ503517		GQ503588
Breynia asteranthos	Esser 99-13 (L)	EU623565		GQ503501	EU643751	
Breynia bicolor	Esser 99-21 (L)	EU623567		GQ503503	EU643754	
Breynia brevipes	Middleton et al. 974 (L)	EU623568			EU643755	
Breynia cf. macrantha	Bouman & Yong RWB050 (HITBC)	MN915813	MN904190	MN915297	MN916081	MN915580
Breynia discigera	Takeuchi et al. 18873 (L)	EU623550	GQ503410		EU643736	
Breynia discocalyx	Beusekom & Phengklai 566 (L)	GQ503387			EU643757	GQ503569
Breynia disticha (1)	Bouman & Verwijs RWB024 (L)	MN915814	MN904191	MN915298	MN916082	MN915581
Breynia disticha (2)	Yu 63 (L)	MN915815	MN904192	MN915299	MN916083	MN915582
Breynia fruticosa	Bouman et al. RWB025 (L)	MN915816	MN904193	MN915300	MN916084	MN915583
Breynia garrettii	Sino-American Guizhou Botanical Expedition 1872 (L)	EU623570	GQ503444	GQ503507	EU643760	GQ503572

Breynia glauca	Pooma et al. 2702 (L)	EU623551	GQ503411		EU643737	GQ503532
Breynia hirsuta	Larsen et al. 33993 (P)	GQ503391	GQ503445		EU643762	
Breynia kerrii	Van Beusekom & Phengklai 1065 (P)	EU623574	GQ503452		EU643764	GQ503579
Breynia lanceolata	Esser 2001-4 (L)	EU623584			EU643774	
Breynia lithophila	Phonsena et al. 5595 (L)		GQ503464	GQ503522		GQ503595
Breynia macrantha	Telford & Bruhl 13107 (L)	GQ503396				
Breynia macrantha	Maxwell 95-1125 (L)				MT551232	
Breynia micrasterias	Erwin & Chai S 27479 (L)	EU623578	GQ503455		EU643768	GQ503582
Breynia novoguineensis*	Baker et al. 37 (L)	EU623549	GQ503409	GQ503472		GQ503530
Breynia oblongifolia	Forster 32745 (NE)	GQ503355	GQ503414	GQ503475		GQ503534
Breynia orbicularis	Soejarto & Southavong 10792 (L)	EU623580	GQ503456	GQ503513	AY936645	GQ503584
Breynia poomae	Phonsena et al. 5245 (L)	EU623582	GQ503457	GQ503515	EU643771	GQ503586
Breynia repens	Middleton et al. 2287 (L)	GQ503385				GQ503566
Breynia retusa	Kathriarachchi et al. 43 (K)				AY936565	
Breynia retusa	Soejarto & Southavong 10783 (L)	GQ503358	GQ503417	GQ503477		GQ503536
Breynia rostrata	Bouman & Yong RWB055 (HITBC)	MN915817	MN904194	MN915301	MN916086	MN915585
Breynia similis (1)	Larsen et al. 46639 (L)	GQ503399	GQ503462	GQ503520	EU643778	GQ503592
Breynia similis (2)	Bouman & Yong RWB054 (HITBC)	MN915818	MN904195	MN915302	MN916085	MN915584
Breynia sp. (1)	Middleton 1715 (L)	MN915843	MN904215	MN915327	MN916112	MN915600
Breynia sp. (2)	Tagane et al. T570 (L)	MN915844	MN904216	MN915328	MN916113	
Breynia spatulifolia	Wong s.n. (L)	EU623588		GQ503523	AY936647	GQ503596
Breynia stipitata	Chase 14461 (K)				AY552422	

Breynia stipitata	Bruhl 2478 (NE)	GQ503359	GQ503418	GQ503478		GQ503537
Breynia thorelii	Van Welzen 2006-1 (L)	EU623590	GQ503468	GQ503526	EU643782	GQ503600
Breynia thyrsiflora	Kostermans 765 (L)	EU623591	GQ503469	GQ503527	EU643783	GQ503601
Breynia vestita	Barker & Beaman 70 (L)	EU623553	GQ503419	GQ503480	EU643738	GQ503540
Breynia villosa	Phengklai et al. 12122 (BKF)	EU623593			EU643786	
Breynia vitis-idea (1)	Tagane et al. V388 (L)	MN915819	MN904184	MN915303	MN916087	
Breynia vitis-idea (2)	Tagane et al. V404 (L)	MN915820	MN904185	MN915304	MN916088	MN915586
Breynia vitis-idea (3)	Majaducon 5676 (L)	MN915821	MN904186	MN915305	MN916089	
Breynia vitis-idea (4)	Yu 157 (L)	MN915822	MN904187	MN915306	MN916090	MN915587
Bridelia tomentosa	Bouman & Yong RWB063 (HITBC)		MN904196	MN915307	MN916359	
Cathetus aff. fasciculatus (1)	Bouman & Yong RWB052 (HITBC)	MN915840	MN904250	MN915324	MN916144	MN915601
Cathetus aff. fasciculatus (2)	Bouman & Yong RWB065 (HITBC)	MN915841	MN904251	MN915325	MN916145	MN915602
Cathetus aff. fasciculatus (3)	Bouman & Yong RWB060 (HITBC)	MN915842	MN904252	MN915326	MN916146	MN915603
Cathetus beckleri	Hosking 2680 (NE)	MN915861	MN904231	MN915347	MN916127	MN915618
Cathetus chrysanthus	Munzinger & McPherson 796 (MO)	AY936680			AY936585	
Cathetus fasciculatus	Bouman et al. RWB026 (L)	MN915895	MN904262	MN915384	MN916154	MN915648
Cathetus distichus	Harold st. John 17.985 (L)	MN915912	MN904276	MN915404	MN916163	MN915665
Cathetus exilis	Hunter et al. 1528 (L)	MN915922	MN904283		MN916362	MN915672
Cathetus filicaulis	Telford 13516 (NE)	MN915923	MN904284	MN915415	MN916170	MN915673
Cathetus gardnerianus	Kathriarachchi et al. 42 (K)	AY936694	MN904314	MN915429	AY936598	MN915684

Cathetus glaucophyllus (1)	Van der Brugt 1156 (WAG)	MN915938	MN904317	MN915432	MN916183	MN915687
Cathetus glaucophyllus (2)	Haba 123 (WAG)	MN915939	MN904318	MN915433	MN916340	MN915688
Cathetus kerstingii (1)	Darbyshire 562 (WAG)	MN915950	MN905074	MN915447	MN916189	MN915701
Cathetus kerstingii (2)	Malaisse 14792 (WAG)	MN915951		MN915448		MN915702
Cathetus myrtifolius (1)	Bouman & Liu RWB034 (L)	MN915995	MN904370	MN915495	MN916214	MN915736
Cathetus myrtifolius (2)	Bouman & Yong RWB053 (HITBC)	MN915996	MN904371	MN915496	MN916215	MN915737
Cathetus myrtifolius (3)	Yu 58 (L)	MN915997	MN904372		MN916216	MN915738
Cathetus patentipilis*	Bruhl 1810 (NE)	MN916020	MN904392	MN915518	MN916234	MN915759
Cathetus petraeus	Blyden 1037 (WAG)	MN916026	MN904397	MN915524	MN916239	MN915763
Cathetus recurvatus	Wilson 612 (NE)	MN916046	MN904414	MN915543	MN916258	MN915778
Cathetus simplex (1)	Bouman RWB069 (L)	MN916074	MN904440	MN915572	MN916276	MN915805
Cathetus simplex (2)	Bouman RWB070 (L)	MN916075	MN904441	MN915573	MN916277	MN915806
Cathetus ussuriensis	Kawakita 124 (KYO)		FJ235366		FJ235274	
Cathetus virgatus	Wrigley & Telford 46642 (K)	AY936738	MN904442	MN915574	AY936639	MN915807
Cathetus welwitschianus	Bidgooet et al. 1882 (K)	AY936739			AY936640	
Cathetus wheeleri	Kathriarachchi et al. 33 (K)	AY936740	MN904445	MN915577	AY936641	MN915810
Cicca ambatovolanus	Randriamampionona et al. 51 (K)	MN915848	MN904218	MN915332	MN916115	MN915605
Cicca ankarana	Ralimanana et al. 663 (K)	MN915851	MN904221	MN915335	MN916118	MN915608
Cicca ankaratrae	Rakotonasolo & Zachary 802 (K)	MN915852	MN904222	MN915336	MN916119	MN915609
Cicca bernieranus	Phillipson 5373 (K)	MN915862	MN904232	MN915348	MN916128	MN915619
Cicca betsileanus	Labat 2402 (K)	MN915863	MN904233	MN915349	MN916360	MN915620

Cicca chacoensis	Krapovickas et al. 45628 (K)	AY936677			AY936582	
Cicca cryptophila	Dumetz 593 (WAG)	MN915899	MN904265	MN915390	MN916358	MN915653
Cicca delpyana (1)	Kami 1215 (WAG)	MN915906		MN915397	MN916161	MN915659
Cicca delpyana (2)	M'Boungou 659 (WAG)		MN904272	MN915398	MN916160	
Cicca elsiae	Davidse & Gonzalez 13359 (L)	MN915916	MN904278	MN915408	MN916337	MN915667
Cicca engleri	Mwangulango 1138 (WAG)		MN905066	MN915410	MN916168	MN915669
Cicca humbertii	Kawakita 235 (KYO)		FJ235345		FJ235253	
Cicca kidna	Cheek 11531	FR715993			FR715992	
Cicca lichenisilvae	Antilahimena 7638 (MO)		MN904343	MN915464	MN916199	
Cicca mantadiensis (1)	Rasoazanany 110 (MO)	MN915979	MN904353	MN915479	MN916204	
Cicca mantadiensis (2)	Rasoazanany 514 (MO)	MN915980	MN904354	MN915480	MN916319	
Cicca marojejiensis	Kawakita 243 (KYO)		FJ235346		FJ235254	
Cicca oreichtitus	Antilahimena 4824 (MO)	MN916013	MN904385		MN916226	
Cicca perrieri	Rakotonasolo et al. 814 (K)	MN916024	MN904395	MN915522	MN916238	MN915762
Cicca philippioides	Ralimanana et al. 627 (K)	MN916027	MN904398	MN915525	MN916240	MN915764
Cicca physocarpa	McPherson 16148 (WAG)	MN916030	MN904401	MN915528	MN916243	MN915766
Cicca pinnata	Mav 1580 (K)	MN916032	MN904403	MN915530	MN916245	MN915704
Cicca polyantha	Breteler 1938 (WAG)	MN916033		MN915531	MN916246	MN915767
Cicca sambiranensis	Bürki et al. 3 (K)	MN916053	MN904421	MN915552	MN916315	MN915784
Cicca sp.	Ravelonarivo 3808 (MO)	MN915845	MN904295	MN915329	MN916282	
Moeroris vakinankaratrae	Ralimanana et al. 435 (K)	AY936737			AY936638	
Dendrophyllanthus aff. Comptonii	Munzinger 608 (MO)	MN915839	MN904214	MN915323	MN916111	
Dendrophyllanthus bourgeoisii	McMillan 5201 (WAG)	MN915870	MN905064	MN915357	MN916134	

Dendrophyllanthus bupleuroides	Mcpherson 18692 (MO)	MN915872	MN904237	MN915359	MN916136	
Dendrophyllanthus castus (1)	Mackee 16581 (L)	MN915879	MN904246	MN915367	MN916327	MN915632
Dendrophyllanthus castus (2)	Mcpherson 19255 (MO)	MN915880	MN904245	MN915368	MN916304	
Dendrophyllanthus caudatus	Kawakita 278 (KYO)		FJ235351		FJ235259	
Dendrophyllanthus chamaecerasus	Munzinger & McPherson 573 (MO)	AY936678			AY936583	
Dendrophyllanthus clamboides	Forster 26376 (L)	MN915893	MN904260	MN915382	MN916152	MN915646
Dendrophyllanthus cuscutiflorus	Yu 61 (L)	MN915901	MN904268	MN915392	MN916299	MN915654
Dendrophyllanthus dallachyanus	Forster 32938 (NE)			MN915393	MN916298	MN915655
Dendrophyllanthus dzumacensis	Jaffre 2412 (L)	MN915913	MN905065	MN915405	MN916164	MN915666
Dendrophyllanthus erwinii	Mitchell PRP1456 (NE)	MN915920	MN904281	MN915413	MN916338	
Dendrophyllanthus favieri	McPherson & Munzinger 18028 (MO)	AY936690			AY936596	
Dendrophyllanthus finschii	Takeuchi & Ama 15603 (L)	MN915924	MN904285	MN915416	MN916171	MN915674
Dendrophyllanthus guillauminii	Kawakita 273 (KYO)		FJ235353		FJ235261	

Dendrophyllanthus hypospodius	Bruhl et al. 1123 (L)		GQ503435	GQ503495	EU643744	GQ503559
Dendrophyllanthus kanalensis	McPherson & Van der Werff 17886 (K)	AY936701			AY936604	
Dendrophyllanthus koniamboensis	Kawakita 277 (KYO)		FJ235350		FJ235258	
Dendrophyllanthus koumacensis	McPherson 19163A (MO)	MN915953	MN904331	MN915451	MN916191	
Dendrophyllanthus lacunarius	Bates 62700 (NE)	MN915955	MN904333	MN915453	MN916312	MN915706
Dendrophyllanthus lacunellus	Bates 62500 (NE)	MN915956	MN904334	MN915454	MN916313	MN915707
Dendrophyllanthus ligustrifolius (1)	McPherson 19091 (MO)	MN915965	MN904344	MN915465	MN916310	
Dendrophyllanthus ligustrifolius (2)	McPherson 5025 (L)	MN915966	MN904309	MN915466	MN916311	MN915714
Dendrophyllanthus loranthoides	MacKee 31810 (K)	AY936705			AY936607	
Dendrophyllanthus mangenotii	Kawakita 270 (KYO)		FJ235349		FJ235257	
Dendrophyllanthus pancherianus	McPherson & Munzinger 18264 (K)	AY936721	MN904391	MN915517	AY936623	MN915758
Dendrophyllanthus pilifer	McPherson 18525 (MO)	MN916031	MN904402	MN915529	MN916244	
Dendrophyllanthus poumensis	Mackee 20748 (L)	MN916039	MN904408	MN915537	MN916251	MN915772

Dendrophyllanthus sauropodoides	Forster 29857 (L)	EU623558	GQ503436	GQ503496	EU643745	GQ503560
Dendrophyllanthus serpentinus	Mackee 20770 (L)	MN916057		MN915556		MN915788
Dendrophyllanthus tenuirhachis	Yu & Tutie 165 (L)	MN916068	MN904435	MN915567	MN916271	MN915800
Dendrophyllanthus unifoliatus	Veillon 7986 (L)	AY936734			AY936635	
Dendrophyllanthus vulcani	Kawakita 274 (KYO)		FJ235354		FJ235262	
Emblica sp.	Yu 250 (L)	MN915889	MN904253	MN915377	MN916148	MN915640
Emblica pachyphylla (1)	Yahara et al. V3843 (L)	MN915853	MN904223	MN915337	MN916120	
Emblica pachyphylla (2)	Tagane et al. V3863 (L)	MN915854	MN904224	MN915338	MN916121	
Emblica bokorensis	Toyama et al. 1740 (FU)			MN915354	MN916132	
Emblica collinsae	Middleton 3302 (L)	MN915896	MN904263	MN915385	MN916155	MN915649
Emblica columnaris (1)	Fujikawa et al. 095327 (L)		MN904302	MN915387	MN916157	MN915651
Emblica columnaris (2)	Funakoshi et al. 085264 (L)	MN915897		MN915388	MN916283	MN915652
Emblica geoffrayi	Larsen et al. 3259 (L)	MN915936	MN904315	MN915430	MN935816	MN915685
Emblica officinalis (1)	Makino banical garden expedition(2015) 103008	MN915917	MN904279	MN915409	MN916167	MN915668
Emblica officinalis (2)	van Welzen 2003-11 (L)	GQ503378	GQ503434	GQ503494	EU643743	GQ503558
Emblica oxyphylla (1)	Middleton 3191 (L)	MN916018	MN904388	MN915515	MN916232	MN915755
Emblica oxyphylla (2)	Yu 174 (L)	MN916019	MN904389		MN916233	MN915756
Emblica pectinata	Yu 65 (L)	MN916022		MN915520	MN916236	MN915761
Emblica phuquocensis	Tagane et al. 5532 (FU)	MN916029	MN904400	MN915527	MN916242	
Emblica racemosa	Cooray 69090414 (L)	MN916035	MN904405	MN915533	MN916248	MN915769

Emblica rufuschaneyi	Van der Ent (L)		MN904418	MN915547	MN916259	MN915781
Emblica saffordii	Fosberg 59609 (L)	MN916050	MN904419	MN915549	MN916260	
Emblica urinaria (1)	Majaducon 5750 (L)	MN916071	MN904437	MN915569	MN916273	MN915802
Emblica urinaria (2)	Bouman RWB018 (L)	MN916072	MN904438	MN915570	MN916274	MN915803
Flueggea acidoton	**S. Fuentes et al. 868 (B, HAJB)**	**LS975740**			**LS975798**	
Flueggea virosa (1)	Bouman & Yunhong RWB068 (HITBC)	MN915824	MN904197	MN915308	MN916091	
Flueggea virosa (2)	Mitchel 2890 (BRI)	MN915823			MN916104	
Flueggea virosa (3)	Chase 2104 (K)				AY552426	
Flueggea virosa (3)	Larsen et al. 45328 (L)		GQ503420	GQ503481		
Flueggea virosa (4)	Yu 64 (L)	MN915825	MN904198		MN916092	MN915588
Glochidion benthamianum	Bruhl 1026 (NE)	GQ503363		GQ503482		GQ503541
Glochidion carinatum	Toyama et al. 3212 (FU)		MN904243	MN915363	MN916138	
Glochidion ellipticum (1)	Bouman & Yong RWB058 (HITBC)	MN915826	MN904199	MN915310	MN916093	MN915589
Glochidion ellipticum (2)	Bouman & Yong RWB061 (HITBC)	MN915827	MN904200	MN915311	MN916094	MN915590
Glochidion ellipticum (3)	Bouman & Yong RWB062 (HITBC)	MN915829	MN904202	MN915309	MN916096	MN915591
Glochidion eriocarpum	Bouman et al. RWB027 (L)	MN915828	MN904201		MN916095	MN915592
Glochidion ferdinandi	Bruhl 2457 (NE)	GQ503366	GQ503421	GQ503484		GQ503543
Glochidion harveyanum	Bruhl 2527 (NE)	GQ503368	GQ503423	GQ503486		GQ503545
Glochidion kaweesakii	Pornpongrungrueng & Triyuttachai 1174 (KKU)	KY091120			KY091108	

Glochidion lanceolarium	Bouman & Yong RWB064 (HITBC)	MN915830	MN904203	MN915312	MN916097	MN915593
Glochidion lanceolatum	Kawakita 116 (KYO)	AY525687	FJ235327		FJ235235	
Glochidion lobocarpum	Bruhl 1146 (NE)	GQ503371	GQ503424	GQ503488		GQ503548
Glochidion mirabilis	Sirichamorn YSM 2009-05 (L)	HM132100	HM132101	HM132099		HM132102
Glochidion philippicum	Forster 29379 (NE)	GQ503373	GQ503426	GQ503490		GQ503550
Glochidion puberum	Chase 11460 (K)	AY936659			AY552428	
Glochidion roseum	Kawakita 143 (KYO)	KC913110	FJ235332		FJ235240	
Glochidion sphaerogynum (1)	Van der Scheur 128 (L)	MN915831	MN904204	MN915313	MN916280	MN915594
Glochidion sphaerogynum (2)	Van Welzen 2003-21 (L)	EU623555	GQ503427		EU643740	GQ503551
Glochidion wrightii	Bouman & Liu RWB032 (L)	MN915832	MN904205	MN915314	MN916098	MN915595
Heterosavia bahamensis	Wurdack D048 (US)	AY936749	AY830381		AY830284	
Kirganelia baccata	Mitchell PRP1514 (NE)			MN915342	MN916126	MN915613
Kirganelia castica	Wolhauser SW60172 (WAG)	MN915878	MN904244	MN915366	MN916141	
Kirganelia ciccoides	Paijmans 2876 (DAV)	MN915891			MN916150	
Kirganelia dinklagei (1)	Bissiengou (WAG)	MN915908	MN904273	MN915399	MN916333	MN915660
Kirganelia dinklagei (2)	Maas 9993 (WAG)	MN915909	MN904274	MN915400	MN916334	MN915661
Kirganelia flexuosa (1)	Chow 132 (L)	MN915927	MN904289	MN915419	MN916173	MN915677
Kirganelia flexuosa (2)	Mcnamara 162 Living collection Berkeley	MN915928	MN904290	MN915420	MN916174	MN915678
Kirganelia flexuosa (3)	Aung et al. 092433 (MBK)	MN915929	MN904288	MN915421	MN916172	MN915679
Kirganelia fuscolurida (1)	Dorr 3650 (WAG)	MN915933	MN905068	MN915425	MN916180	
Kirganelia fuscolurida (2)	Schatz 1737 (WAG)	MN915934	MN904296	MN915426	MN916179	

Kirganelia glauca	Bouman & Liu RWB028 (L)	MN915940	MN904291	MN915434	MN916175	MN915689
Kirganelia matitanensis	Ravelonarivo 4276 (MO)	MN915981	MN904355	MN915481	MN916205	
Kirganelia microcarpa (1)	Bouman & Yong RWB056 (HITBC)	MN915985	MN904358	MN915483	MN916207	MN915729
Kirganelia microcarpa (2)	Yang et al. V2332 (L)	MN915986	MN904359	MN915484	MN916356	
Kirganelia microcarpa (3)	Tanaka et al. MY112 (L)	MN915987	MN904360	MN915485	MN916346	
Kirganelia microcarpa (4)	Yahara et al. 4346 (L)		MN904361	MN915486	MN916208	
Kirganelia muelleriana (1)	Kew Seed bank collection 145024	MN915991	MN904366	MN915491	MN916295	
Kirganelia muelleriana (2)	Bingham 6893 (WAG)	MN915992	MN904368	MN915492	MN916212	MN915734
Kirganelia muelleriana (3)	Jongkind 39824 (WAG)	MN915993	MN904367	MN915493	MN916211	MN915735
Kirganelia muelleriana (4)	Wieringa 7074 (WAG)	MN915994	MN904369	MN915494	MN916213	
Kirganelia novae-hollandiae	Telford 13024 (NE)	MN916001	MN904376	MN915500	MN916219	MN915741
Kirganelia oligosperma	Kawakita 101 (KYO)		FJ235360		FJ235268	
Kirganelia ovalifolia (1)	Mallaisse 12688 (WAG)	MN916014	MN904312	MN915512	MN916227	MN915751
Kirganelia ovalifolia (2)	de Wilde 7622 (WAG)	MN916015		MN915513	MN916228	MN915752
Kirganelia ovalifolia (3)	Friis 13337 (WAG)	MN916016	MN904301	MN915514	MN916229	MN915753
Kirganelia pervilleana (1)	Hoffmann et al. 392 (K)	AY936723			AY936625	
Kirganelia pervilleana (2)	Randrianasolo 526 (MO)	MN916025	MN904396	MN915523	MN916351	
Kirganelia polypserma (1)	Kew seed bank HBL20160135 (Kew seed bank 174282)	MN916037	MN904406	MN915535	MN916249	

Kirganelia polypserma (2)	Saolomao 40 (WAG)	MN916038	MN904407	MN915536	MN916250	MN915770
Kirganelia polypserma (3)	Friis 10341 (WAG)	MN916036	MN904386	MN915534	MN916230	MN915771
Kirganelia purpurea	Ward et al. 10442 (K)	MN916042	MN904411	MN915540	MN916254	MN915775
Leptopus chinensis	Brownless (L)	MN915833	MN904206	MN915315	MN916099	
Lingelsheimia sp.	Rabenantoandro et al. 1115 (MO)	AY936662	AY830375		AY830272	
Lysiandra calycina	Chase MWC 2163 (K)	AY936674	AY579869		AY552446	
Lysiandra carpentariae	Clarkson & Neldner 8410 (L)	MN915877	MN905063	MN915365	MN916140	MN915631
Lysiandra cauticola	Mitchell 837 (NE)	MN915881	MN904247	MN915369	MN916303	MN915633
Lysiandra cf. carpentariae	Hyland 8033 (L)	MN915888	MN904256	MN915376	MN916147	MN915639
Lysiandra collina	Telford & Bruhl 13119 (L)		MN904264	MN915386	MN916156	MN915650
Lysiandra flagellaris	Fryxell & Craven (L)	MN915926	MN904287	MN915418	MN916307	MN915676
Lysiandra fuernrohrii	Coveny 13478 (NE)		MN904294		MN916178	
Lysiandra grandisepala	Albrecht 13268 (NE)	MN915942	MN904319	MN915436	MN916289	MN915690
Lysiandra graniticola*	Telford 13004 (NE)	MN915943	MN904320	MN915437	MN916185	MN915691
Lysiandra gunnii	Coveny 11474 (L)	MN915944	MN904322	MN915439	MN916290	MN915693
Lysiandra hebecarpa	Copeland NE66669 (NE)		MN904324		MN916308	MN915695
Lysiandra hirtella	Pedersen 1328 (L)	MN915947	MN904326	MN915442	MN916187	MN915697
Lysiandra microclada	Telford 13038 (L)	MN915988	MN904362	MN915487	MN916320	MN915730
Lysiandra mitchelii	Bruhl 1919B (NE)	MN915990	MN904365	MN915490	MN916210	MN915733
Lysiandra subcrenulata	Streimann s.n. (L)	MN916063	MN904432		MN916270	MN915795
Lysiandra trachygyne	Egan 2886 (NE)	MN916069	MN904436	MN915568	MN916294	MN915801
Margaritaria anomala	Ramison 413 (MO)	MN915834			MN916100	

Margaritaria discoidea (1)	Nicholson 1 (L)		MN904208	MN915317	MN916102	
Margaritaria discoidea (2)	Nicholson s.n. (L)		MN904207	MN915316	MN916101	
Margaritaria dubiumtraceyi	Forster 29387 (BRI)			MN935815	MN916103	
Margaritaria indica	Orr 80532		MN904209	MN915318	MN916105	
Margaritaria nobilis	Orr 875422		MN904210	MN915319	MN916106	MN915596
Margaritaria rhomboidalis	Rabenantoandro et al. 656 (K)	AY936665			AY936571	
Margaritaria sp. Uganda	Nicholson 3a (L)	MN915835	MN904211	MN915320	MN916107	MN915597
Moeroris sp.	Ravelonarivo 4264 (MO)	MN915846		MN915330	MN916281	
Moeroris amara (1)	van Welzen 2006-5(L)	EU623557	GQ503433	GQ503493	EU643742	GQ503557
Moeroris amara (2)	Wieringa 8189 (WAG)	MN915847	MN904217	MN915331	MN916114	
Moeroris arenaria	Worthington 18323 (L)	AY936743	AY830380		AY830280	
Moeroris boehmii (1)	Gereau 5007 (WAG)	MN915864	MN904254	MN915350	MN916302	MN915621
Moeroris boehmii (2)	Wieringa 8841 (WAG)	MN915865	MN904234	MN915351	MN916129	MN915622
Moeroris boehmii (3)	Bidgood 6838 (WAG)	MN915866	MN904235	MN915352	MN916130	MN915623
Moeroris boehmii (4)	Lisowski 13765 (WAG)	MN915867	MN904303	MN915353	MN916131	MN915624
Moeroris bongensis*	de Wilde 7858 (WAG)	MN915868	MN904305	MN915355	MN916284	
Moeroris caesiifolia	Cheek 10376 (WAG)	MN915875	MN904242	MN915362	MN916137	MN915629
Moeroris ceratostemon	Bidgood 6776 (WAG)	MN915882	MN904248	MN915370	MN916142	MN915634
Moeroris cf. boehmii	Friis 13159 (WAG)	MN915883	MN904249	MN915371	MN916143	MN915635
Moeroris cf. fischeri	de Wilde 4391 (WAG)	MN915887	MN905067	MN915375	MN916343	MN915725
Moeroris cf. rotundifolia	Nicholson 2 (L)		MN904329	MN915446	MN916342	MN915700

Moeroris coursii	Razafindrahaja 184 (MO)	MN915898	MN904266	MN915389	MN916329	
Moeroris debilis (1)	Bouman & Liu RWB037 (L)	MN915903	MN904269	MN915394	MN916330	MN915656
Moeroris debilis (2)	Bouman RWB071 (L)	MN915904	MN904270	MN915395	MN916331	MN915657
Moeroris debilis (3)	Kamarudim & Apok (L)	MN915905	MN904271	MN915396	MN916332	MN915658
Moeroris dimorpha	**E.R. Bcquer et al. HFC 87940 (HAJB)**	**LS975738**			**LS975795**	
Moeroris dinteri (1)	Dinter 213 (WAG)	MN915910		MN915401	MN916335	MN915662
Moeroris dinteri (2)	Oliver 6543 (WAG)	MN915911	MN905069	MN915402	MN916336	MN915663
Moeroris fischeri	Gereau 1996 (WAG)	MN915925	MN904286	MN915417		MN915675
Moeroris fraterna	Nooteboom 3010 (L)	MN915931		MN915423	MN916306	MN915681
Moeroris friesii	Harder et al. 2778 (WAG)	MN915932	MN904293	MN915424	MN916177	MN915682
Moeroris fuertesii	**S. Fuentes et al. 294 (B, HAJB)**	**LS975752**			**LS975812**	
Moeroris gabonensis (1)	Maas 10095 (WAG)		MN904299	MN915427	MN916181	MN915683
Moeroris gabonensis (2)	Wieringa 8492 (WAG)	MN915935	MN904313	MN915428	MN916182	
Moeroris gillettiana	Germishuizen 9727 (WAG)	MN915937	MN904316	MN915431		MN915686
Moeroris harrisii	Faulkner 3179 (WAG)	MN915945	MN904323	MN915440	MN916341	MN915694
Moeroris hutchinsoniana (1)	Poilecot 7974 (K)	AY936697	MN904327	MN915443	AY936601	MN915698
Moeroris hutchinsoniana (2)	Bamps 88 (WAG)	MN915948	MN904306	MN915444		
Moeroris kaessneri	Pocs 89182 (K)	AY936700			AY936603	
Moeroris leucantha (1)	de Wilde 4604 (WAG)	MN915962	MN904300	MN915460	MN916149	MN915642
Moeroris leucantha (2)	Friis 8619 (WAG)	MN915963	MN904340	MN915461	MN916344	MN915713
Moeroris leucocalyx (1)	Bidgood 7161 (WAG)		MN904341	MN915462	MN916197	
Moeroris leucocalyx (2)	Bidgood 6969 (WAG)	MN915964	MN904342	MN915463	MN916198	

Moeroris limmuensis	de Wilde 6524 (WAG)	MN915967	MN904345	MN915467	MN916291	MN915715
Moeroris loandensis (1)	Pawek R597 (WAG)	MN915968	MN904346	MN915469	MN916201	MN915717
Moeroris loandensis (2)	Pawek 12535 (WAG)	MN915970	MN904297	MN915470	MN916202	MN915718
Moeroris loandensis (3)	Nuvunga 526 (WAG)	MN915969	MN905072	MN915471	MN916203	MN915719
Moeroris lokohensis	Antilahimena 8041 (MO)	MN915971	MN904347		MN916316	
Moeroris macrantha	Biegel et al. 4847 (WAG)	MN915972	MN905075	MN915472	MN916292	MN915720
Moeroris madagascariensis	McPherson 18925 (MO)	MN915973	MN904348	MN915473	MN916317	
Moeroris maderaspatensis	Hunter et al. 1532 (K)	AY936707			AY936609	
Moeroris magnificens	van der Burgt 1196 (WAG)	MN915975	MN904349	MN915475	MN916345	MN915722
Moeroris manniana (1)	Raynal 12256 (WAG)	MN915977	MN904351	MN915477	MN916347	MN915724
Moeroris manniana (2)	Biye 129 (WAG)	MN915978	MN904352	MN915478		MN915726
Moeroris melleri	Lowry et al. 5814 (K)	MN915983	MN904357	MN915482	MN916314	MN915728
Moeroris nirurioides (1)	Bidgood 8049 (WAG)	MN915998	MN904374	MN915497	MN916305	MN915739
Moeroris nirurioides (2)	Wieringa 7502 (WAG)	MN915999	MN904375	MN915498	MN916218	MN915740
Moeroris nummulariifolia (1)	Nicholson 3b (L)	MN916002	MN904377	MN915501	MN916288	MN915742
Moeroris nummulariifolia (2)	Wieringa 8374 (WAG)	MN916003	MN904380	MN915502	MN916361	MN915744
Moeroris nummulariifolia (3)	van Andel 5732 (WAG)	MN916004	MN904381	MN915503	MN916223	MN915743
Moeroris nummulariifolia (4)	Mwangoka 5900 (WAG)	MN916005	MN904379	MN915504	MN916222	
Moeroris nummulariifolia (5)	Razafitsalama 235 (MO)	MN916006	MN904378	MN915505	MN916220	

Moeroris nummulariifolia (6)	Blaxell 1118 (U)	MN916007	MN904310	MN915506	MN916221	MN915745
Moeroris nyale	Etuge 4453 (WAG)	MN916008	MN904382	MN915507	MN916224	MN915746
Moeroris odontadenia (1)	Darbyshire 207 (WAG)	MN916009	MN904311	MN915508	MN916348	MN915747
Moeroris odontadenia (2)	Bouman & Verwijs RWB025 (L)	MN916010	MN904383	MN915509	MN916349	MN915748
Moeroris odontadenia (3)	Wieringa 7665 (WAG)	MN916011	MN904384	MN915510	MN916350	MN915749
Moeroris oxycoccifolia	Gereau 5219 (WAG)	MN916017	MN904387		MN916231	MN915754
Moeroris paxii	Bidgood 2983 (WAG)	MN916021	MN904393	MN915519	MN916235	MN915760
Moeroris pentandra	Kew Seed bank collection 519962	MN916023	MN904394	MN915521	MN916237	
Moeroris phillyreifolia	van Nek 2188 (WAG)	MN916028	MN904399	MN915526	MN916241	MN915765
Moeroris procera (1)	**S. Fuentes et al. 428 (B, HAJB)**	**LS975737**			**LS975794**	
Moeroris procera (2)	**S. Fuentes et al. 414 (B, HAJB)**	**LS975769**			**LS975830**	
Moeroris rangoloakensis	Schatz et al. 3709 (K)	MN916045	MN904413	MN915542	MN916257	MN915777
Moeroris rheedii	Kathriarachchi et al. 1 (K)	AY936729	MN904415	MN915544	AY936630	MN915779
Moeroris rotundifolia	Wieringa 8849 (WAG)	MN916047	MN904416	MN915545	MN916352	MN915780
Moeroris sepialis	Luke 7112 (K)	AY936732			AY936633	
Moeroris stipulata (1)	Jansen-Jacobs 2813 (U)		MN904430	MN915561	MN916268	MN915793
Moeroris stipulata (2)	Gieteling 114 (WAG)	MN916062	MN904431	MN915562	MN916269	MN915794
Moeroris tenella (1)	Bruhl 2633 (L)	MN916065	MN904433	MN915564	MN916354	MN915797
Moeroris tenella (2)	Bouman RWB019 (L)	MN916066	MN904434	MN915565	MN916355	MN915798
Moeroris tenella (3)	Groenendijk 15 (WAG)	MN916067	MN904308	MN915566	MN916357	MN915799
Moeroris wakensis*	Wieringa 5107 (WAG)		MN904443	MN915575		MN915808
Nellica magudensis	Blokhuis 50 (WAG)	MN915976	MN904350	MN915476	MN916318	MN915723
Nellica mendoncae	de Wilde 6464 (WAG)	MN915984				
Nellica polygonoides	Kim & Miller 1078 (U)	MN916034	MN904404	MN915532	MN916247	MN915768

Notoleptopus decaisnei	Evans 3222 (K)	AM745836			AM745833	
Notoleptopus decaisnei	Fraser 267 (L)		GQ503431	GQ503491		GQ503555
Nymphanthus balgooyi (1)	Van der Ent	MN915857	MN904227	MN915343	MN916300	MN915614
Nymphanthus balgooyi (2)	Yu 192 (L)	MN915858	MN904228	MN915344	MN916301	MN915615
Nymphanthus balgooyi (3)	Yu 259 (L)	MN915859	MN904229	MN915345	MN916324	MN915616
Nymphanthus balgooyi (4)	Agoo 5700 (L)	MN915860	MN904230	MN915346	MN916325	MN915617
Nymphanthus buxifolius (1)	Yu 163 (L)	MN915873	MN904240	MN915360	MN916326	MN915627
Nymphanthus buxifolius (2)	Yu 167 (L)	MN915874	MN904241	MN915361	MN916285	MN915628
Nymphanthus cf. buxifolius (1)	Agoo 5659 (L)	MN915884	MN904238	MN915372	MN916286	MN915636
Nymphanthus cf. buxifolius (2)	Agoo 5683 (L)	MN915885	MN905070	MN915373	MN916287	MN915637
Nymphanthus cf. buxifolius (3)	Agoo 5738 (L)	MN915886	MN904239	MN915374	MN916328	MN915638
Nymphanthus cf. sootepensis	Bouman & Yong RWB059 (HITBC)	MN915890	MN904428	MN915378	MN916267	MN915643
Nymphanthus curranii	Yu 261 (L)	MN915900	MN904267	MN915391	MN916158	MN915604
Nymphanthus elegans (1)	Yahara et al. V3499 (L)	MN915914		MN915406	MN916165	
Nymphanthus elegans (2)	Yahara et al. V5597 (L)	MN915915	MN904277	MN915407	MN916166	

Nymphanthus floribundus	Kathriarachchi et al. 66 (K)	AY936682	MN904259	MN915381	AY936587	
Nymphanthus glaucescens (1)	Bouman & Yong RWB066 (HITBC)	MN916040	MN904409	MN915538	MN916252	MN915773
Nymphanthus glaucescens (2)	Esser 98-68 (L)	MN916041	MN904410	MN915539	MN916253	MN915774
Nymphanthus gomphocarpus	Klackenberg & Lundin 579 (L)	MN915941	MN905073	MN915435	MN916184	
Nymphanthus kinabalucius	Van der Ent (Kinabalu Parcs living collection)	MN915952	MN904330	MN915449	MN916190	MN915703
Nymphanthus laciniatus	Agoo 5660 (L)	MN915954	MN904332	MN915452	MN916192	MN915705
Nymphanthus leptoclados	Bouman & Yong RWB051 (HITBC)	MN915961	MN904339	MN915459	MN916196	MN915712
Nymphanthus longifolius	TRP-5004102 (BK)	AB550090				
Nymphanthus megalanthus	Calaramo (L)	MN915982	MN904356		MN916206	MN915727
Nymphanthus ruber	Lee et al. s.n. (CUHK)	AY765298				
Nymphanthus rubescens	Yahara et al. V2902 (L)	MN916048	MN904417	MN915546	MN916322	
Nymphanthus sootepensis (1)	Makino banical garden expedition(2015) 103251	MN916059	MN904426	MN915558	MN916297	MN915790
Nymphanthus sootepensis (2)	Makino banical garden expedition(2015) 103753	MN916060	MN904427	MN915559	MN916266	MN915791
Nymphanthus tetrandrus	Fujikawa et al. 053175 (L)	MN916058	MN904425	MN915557	MN916296	MN915789
Nymphanthus watsonii	Yu 225 (L)	MN916076	MN904444	MN915576	MN916278	MN915809
Phyllanthus acidus	van welzen 2003-14(L)	MN915836	GQ503432	GQ503492	MN916108	GQ503556

Phyllanthus acuminatus (1)	Breteler 4238 (WAG)	MN915837	MN904212	MN915321	MN916109	MN915598
Phyllanthus acuminatus (2)	Wallnöfer 6031 (U)	MN915838	MN904213	MN915322	MN916110	MN915599
Phyllanthus aeneus	Kawakita 272 (KYO)		FJ235352		FJ235260	
Phyllanthus angustifolius	Lauerer 091479	MN915849	MN904219	MN915333	MN916116	MN915606
Phyllanthus anisolobus	Liesner 14363 (U)	MN915850	MN904220	MN915334	MN916117	MN915607
Phyllanthus arbuscula	Reynders19074182 (L)	MN915855	MN904226	MN915339	MN916123	MN915610
Phyllanthus arenicola	Maas & Carauta (U)		MN905071	MN915340	MN916124	MN915611
Phyllanthus attenuatus	Breteler 4696 (WAG)	MN915856	MN904304	MN915341	MN916125	MN915612
Phyllanthus botryanthus	de Wilde 31 (WAG)	MN915869	MN904255	MN915356	MN916133	MN915625
Phyllanthus brasiliensis	Ule 6408 (L)	MN915871	MN904236	MN915358	MN916135	MN915626
Phyllanthus caroliniensis	Groenendijk 55 (WAG)	MN915876		MN915364	MN916139	MN915630
Phyllanthus cf.klotzschianus	Carneiro 10 (K)			MN915450		MN915641
Phyllanthus chamaecristoid	van Ee et al. 404 (K)	AY936679			AY936584	
Phyllanthus chryseus	Van Ee et al. 387 (K)	AY936681	MN904257	MN915379	AY936586	MN915644
Phyllanthus cinctus	Ekman 19166 (K)	MN915892	MN904258	MN915380	MN916151	MN915645
Phyllanthus claussenii	Hatschbach 64117 (U)	MN915894	MN904261	MN915383	MN916153	MN915647
Phyllanthus comosus	Gutierrez et al. 81777 (WIS)	AY936685			AY936590	
Phyllanthus comosus (2)	**T. Borsch et al. 4271 (B, HAJB)**	**LS975727**			**LS975785**	
Phyllanthus dawsonii	da Silva 2073 (DAV)	MN915902			MN916159	
Phyllanthus dictyospermus	Santos 5712 (DAV)	MN915907			MN916162	

Phyllanthus discolor	Berazain et al. 71878 (K)	AY936688	MN904275	MN915403	AY936593	MN915664
Phyllanthus epiphyllanthus (1)	Lauerer 080405	MN915918	MN904225	MN915411	MN916122	MN915670
Phyllanthus epiphyllanthus (2)	Reynders IPEN:XX-0-BR-19840633 (L)	MN915919	MN904280	MN915412	MN916169	MN915671
Phyllanthus evanescens	Stevens 32461 (MO)	MN915921	MN904282	MN915414	MN916339	
Phyllanthus excisus	**W. Greuter et al. 28281 (B, HAJB, P-Gr)**	**LS975746**			**LS975806**	
Phyllanthus fluitans	Krämer xx-0-Dath-518 (L)	MN915930	MN904292	MN915422	MN916176	MN915680
Phyllanthus graveolens	Klitgaard et al. 399 (K)	AY936696	MN904321	MN915438	AY936600	MN915692
Phyllanthus heliotropus	Maas et al. 7762 (U)	MN915946	MN904325	MN915441	MN916186	MN915696
Phyllanthus incrustatus	**T. Borsch et al. 4504 (B, HAJB)**	**LS975731**			**LS975788**	
Phyllanthus juglandifolius	Bouman RWB16	MN915949	MN904328	MN915445	MN916188	MN915699
Phyllanthus klotzschianus	Grappo et al. 780 (K)	AY936702			AY936605	
Phyllanthus lamprophyllus (1)	Agoo 5592 (L)	MN915957	MN904335	MN915455	MN916193	MN915708
Phyllanthus lamprophyllus (2)	Telford & Bruhl 13049 (L)	MN915958	MN904336	MN915456	MN916194	MN915709
Phyllanthus lamprophyllus (3)	Telford & Bruhl 13051 (L)	MN915959	MN904337	MN915457	MN916195	MN915710
Phyllanthus lamprophyllus (4)	Yu 161 (L)	MN915960	MN904338	MN915458	MN916309	MN915711
Phyllanthus lindenianus	**S. Fuentes et al. 1003 (B)**	**LS975755**			**LS975815**	
Phyllanthus lindenianus	Fuertes 345 (K)			MN915468	MN916200	MN915716
Phyllanthus madeirensis	Vincentini 1206 (U)	MN915974	MN905078	MN915474	MN916293	MN915721

Phyllanthus maleolens	**S. Fuentes et al. 1121 (B)**	**LS975756**			**LS975816**	
Phyllanthus microdictyis	Van Ee 399 (K)	AY936709	MN904363	MN915488	AY936612	MN915731
Phyllanthus mimosoides	Reynders 19074179 (L)	MN915989	MN904364	MN915489	MN916209	MN915732
Phyllanthus mirifcus	**T. Borsch et al. 5021 (B, HAJB)**	**LS975774**			**LS975835**	
Phyllanthus niruri	De la Quintana 333 (MO)	MN916000	MN904373	MN915499	MN916217	
Phyllanthus nummularioides	**S. Fuentes et al. 880 (B)**	**LS975753**			**LS975813**	
Phyllanthus nutans	**S. Fuentes et al. 996 (B)**	**LS975754**			**LS975814**	
Phyllanthus orbicularis	Eschevaria s.n. (L)	MN916012	MN904298	MN915511	MN916225	MN915750
Phyllanthus pachystylus	Van Ee 402 (K)	AY936720	MN904390	MN915516	AY936622	MN915757
Phyllanthus phlebocarpus	**P.A. Gonzalez HFC 87732 (HAJB)**	**LS975758**			**LS975819**	
Phyllanthus pseudocicca (1)	**B. Falcon et al. HFC 87780 (HAJB)**	**LS975736**			**LS975793**	
Phyllanthus pseudocicca (2)	**P.A. Gonzalez HFC 87681 (HAJB)**	**LS975759**			**LS975820**	
Phyllanthus purpusii	Breedlove 42730 Living collection Berkeley	MN916043	MN904412	MN915541	MN916255	MN915776
Phyllanthus ramillosus	Arbo 6945 (DAV)	MN916044			MN916256	
Phyllanthus ruscifolius	Cuatrecasas 21631 (U)	MN916049	MN905077	MN915548		MN915782
Phyllanthus salviifolius (1)	Balslev 1888 (U)	MN916051	MN905076	MN915550	MN916261	
Phyllanthus salviifolius (2)	Jorgensen 61204 (U)	MN916052	MN904420	MN915551	MN916262	MN915783
Phyllanthus sellowianus (1)	Chase 14776	MN916054	MN904422	MN915553	MN916263	MN915785

Phyllanthus sellowianus (2)	Chase 14777	MN916055	MN904423	MN915554	MN916264	MN915786
Phyllanthus sellowianus (3)	Chase 14463	MN916056	MN904424	MN915555	MN916265	MN915787
Phyllanthus sp. sect. Callitrichoides	**B. Falcon et al. HFC 87779 (HAJB)**	**LS975742**			**LS975801**	
Phyllanthus spruceanus	Maas & Maas 474 (U)	MN916061	MN904429	MN915560	MN916353	MN915792
Phyllanthus subcarnosus	**T. Borsch et al. 4707 (B, HAJB)**	**LS975741**			**LS975800**	
Phyllanthus symphoricarpoides	Cuatrecasas 18421 (U)	MN916064	MN904307	MN915563	MN916321	MN915796
Phyllanthus tuerckheinii	Mendez 8022 (DAV)	MN916070			MN916272	
Phyllanthus vacciniifolius	Hokche et al. 854 (U)	MN916073	MN904439	MN915571	MN916275	MN915804
Phyllanthus williamioides	**T. Borsch et al. 4523 (B, HAJB)**	**LS975730**			**LS975787**	
Phyllanthys myrtilloides subsp. Alainii	**S. Fuentes et al. 556 (B, HAJB)**				**LS975799**	
Phyllanthys myrtilloides subsp. Erythrinus	**W. Greuter et al. 28014 (B, HAJB, P-Gr)**	**LS975734**			**LS975791**	
Phyllanthys myrtilloides subsp. Shaferi	**S. Fuentes et al. 426 (B, HAJB)**	**LS975743**			**LS975802**	
Phyllanthys myrtilloides subsp. Spathulifolius	**P.A. Gonzalez HFC 87731 (HAJB)**	**LS975772**			**LS975833**	
Plagiocladus diandrus	Wieringa 2903 (WAG)				AY936592	
Plagiocladus diandrus	de Wilde & de Wilde 11641 (WAG)	AY936687				
Synostemon albiflorus (1)	Forster 32329 (NE)	MN916077	MN904446	MN915578	MN916279	MN915811

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

CHAPTER 9

Multiple continental dispersal events and radiation events underlie the modern-day diversity of tribe Phyllantheae (Phyllanthaceae)

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Submitted for publication in Biological Journal of the Linnaean Society

Chapter 9

Multiple continental dispersal events and radiation events underlie the modern-day diversity of tribe Phyllantheae (Phyllanthaceae)

Short title: Historical biogeography of tribe Phyllantheae

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Abstract

Several hypotheses have been invoked to explain the pantropical distribution of many plant taxa today. In this study, we reconstruct the historical biogeography of the monophyletic tribe Phyllantheae, of which the majority consists of *Phyllanthus* s.l. and study the processes that have given rise to the clade's pantropical distribution. A molecular dataset consisting of two nuclear markers and three plastid markers was analysed in BEAST to reconstruct divergence times for 212 species of tribe Phyllantheae. Ancestral area estimations were performed using the BioGeoBears package as implemented in RASP and the R package 'Bamm' was used to study shifts in species diversification rates. Tribe Phyllantheae originated during the Late Palaeocene close to the Palaeocene-Eocene Thermal Maximum, but we were unable to reconstruct the origin of this group. Fossil evidence from the Eocene in Europe together with the wide distribution of early diverged taxa could hint at a boreotropical origin with early dispersals to Africa, Asia and North America. We detected multiple dispersal events within and between the major clades of tribe Phyllantheae. These occurred sometimes at similar time intervals, which coincide with known dispersal routes, but many dispersal events support an explanation through long-distance dispersal. Species diversity of tribe Phyllantheae is unevenly distributed among clades and a pollination mutualism involving moths has not lead to increased speciation rates in all associated taxa possibly because differences in dispersal vectors might have been a limiting factor.

Keywords: BEAST, boreotropics, diversification rate shifts, *Glochidion*, *Phyllanthus* subgenus *Gomphidium*, molecular dating, Phyllantheae, pollination mutualism

Introduction

Intercontinental disjunctions associated with pantropical plant lineages have been the subject of many studies that generated different explanations with varying biogeographical implications in nonconcurrent timeframes. The presence of older taxa that occur predominantly in the southern hemisphere have been attributed to vicariance driven by plate tectonics after the break-up of Gondwana in the Jurassic (Raven & Axelrod 1974; Nelson & Platnick 1981; Wiley 1988; Humphries & Parenti 1999; Givnish & Renner 2004). Indications from micro- and macrofossil evidence from the Eocene of Europe and North America, have generated the theory of the boreotropical forests (Wolfe 1975; Tiffney 1985). A hypothesized tropical belt in the Northern hemisphere in the Early Eocene during the Paleocene-Eocene Thermal Maximum (PETM), which is supported by fossil evidence (Wolfe 1975). Subsequent cooling in the Late Eocene shifted the tropical belt closer to the equator, causing plant taxa to disperse and become isolated in Africa, Asia and North America (Wolfe 1975; Zachos et al. 2001). Boreotropical patterns have also been observed in plant clades such as Annonaceae (Thomas et al. 2015), Burseraceae (Weeks et al. 2005), Urticaceae (Huang et al. 2019) and the fern genus *Diplazium* Sw. (Wei et al. 2015). However, the boreotropical hypothesis does not account for post-Eocene dispersal events, which have sometimes been explained in the context of the Miocene geodispersal hypothesis (Zhou et al. 2012; van Welzen et al. 2014a), the Antarctic land-bridge between Australia and South America (van den Ende et al. 2017) or long-distance dispersal (Renner et al. 2001). Pantropical taxa present a valuable study subject to evaluate these theories.

The former pantropical plant genus *Phyllanthus* s.l. contained more than 800 species that were organized in eighteen morphologically defined subgenera (Bouman et al. 2018). However, this high species number is not equally distributed among all subgeneric groups and a radiation in some specific groups has been linked to the presence of mutualistic moths as pollinators (Kato et al. 2003; Kawakita & Kato 2004a; Kawakita & Kato 2009). The genus was found to be paraphyletic and nested within it were the Australasian genera *Breynia* J.R.Forst. & G.Forst., *Glochidion* J.R.Forst. & G.Forst. and *Synostemon* F.Muell. (Kathriarachchi et al. 2006; Pruesapan et al. 2012; Bouman et al. 2020; Falcón et al. 2020). If combined, *Phyllanthus* s.l. would be a giant genus with more than 1200 species (Hoffmann et al. 2006; van Welzen et al. 2014b). Recent revisions have proposed to split the genus into 10 morphologically distinguishable and monophyletic genera (Bouman et al. 2022), a summary of the new classification is shown in table 9-1. Here we discuss the various taxa according to the new classification while mentioning their treatment in the previously broader definition of *Phyllanthus*.

The species of *Phyllanthus* s.l. are characterized by small unisexual flowers with only sepals, usually nectar disc/glands and many species possess a specialized branching system called phyllanthoid branching (Webster 1956). Species with phyllanthoid branching have their axes specialized in orthotropic branches where the leaves are reduced to scales (cataphylls) and the plagiotropic branchlets are deciduous and they bear laminate leaves (Webster 1956). Several dispersal strategies have been inferred from morphological characters of the seeds and fruits in tribe Phyllantheae. The fruits and seeds are variable and are often diagnostic for specific genera or clades. The majority of fruits are dehiscent capsules that do not require additional dispersal vectors. In a few clades, dispersal by animals (probably birds) is more likely, such as with the bright blue sarcotestal seeds of *Margaritaria* L.f. (Webster 1979) or the berries of *Kirganelia* A.Juss. (*Phyllanthus* subgenus *Kirganelia*, Brunel 1987). Dispersal by large animals is largely unexplored, but could be present in a few species with larger, more indehiscent fruits such as those found in *Cicca* L. (specifically section *Omphacodopsis* (Jean F.Brunel) R.W.Bouman) and possibly in *Emblica* Gaertn. (Prasad et al. 2006). Considering the broader treatment of *Phyllanthus* s.l., this clade has a distribution traditionally attributed to Gondwanan origins, but dated reconstructions suggest that the group originated in the Early Eocene (Kawakita & Kato 2009; Luo et al. 2011; Kawakita et al. 2019). Dispersal events must therefore have occurred after the break-up of Gondwana, but there are few studies that focus on the distribution of *Phyllanthus* s.l. (for a pre-molecular analysis, see Holm-Nielsen 1979). Cai et al. (2019) also found many whole-genome duplication events in the Malpighiales with the majority occurring during the Paleocene-Eocene transition. Although sampling for some families was limited, these genome duplications were hypothesized to be related to subsequent survival under climate change and adaptation to new conditions.

Fossils of *Phyllanthus* s.l. or Phyllanthaceae are scarce, but findings in Asia include Eocene wood (Mehrotra et al. 2010), leaves (Srivastava & Mehrotra 2014; Shukla et al. 2016), pollen (Hofmann et al. 2019) and possibly Cretaceous fruits (Kapgate et al. 2017). Findings from palynological studies from the Early Eocene of Europe at the end of the PETM also found pollen attributed to tribe Phyllantheae (Gruas-Cavagnetto & Köhler 1992; Hofmann et al. 2015; Hofmann & Gregor 2018). Leaf imprints, wood or incomplete fruits and seeds remain difficult to assign with certainty to any specific clade of tribe Phyllantheae due to a lack of diagnostic characters (van Welzen et al. 2015).

Several dispersal events can already be deduced from the molecular phylogeny (see Bouman et al. 2020; Falcón et al. 2020), but have not been studied in a historical and biogeographical context. The aims of this present paper are: (1) to date the existing phylogeny and provide a more detailed exploration than

Table 9-1. Classifications of *Phyllanthus* s.l., left as previously treated as a paraphyletic genus with 17 subgenera (*P.* subgenus *Cyclanthera* (G.L.Webster) G.L.Webster was transferred as a section to P. subgenus *Xylophylla* (Hidalgo et al. 2020), while *P.* section *Lysiandra* was shown to be distinct from *P.* subgenus *Phyllanthus* (Bouman et al. 2021), right following the new classification as presented in Bouman et al. (2022). The numbering of the clades as in Fig. 9-2.

Clade	**Taxa of *Phyllanthus* s.l.**	**New classification sensu Bouman et al. 2022 (genera)**
A	*Phyllanthus* subgenus *Isocladus*	*Nellica*
B1	*Phyllanthus* subgenus *Macraea*	*Cathetus* subgenus *Macraea*
B2	*Phyllanthus* subgenus *Ceramanthus*	*Cathetus* subgenus .
C1	*Phyllanthus* subgenus *Kirganelia*	*Kirganelia*
C3	*Phyllanthus* section *Lysiandra*	*Lysiandra*
C4	*Phyllanthus* subgenus *Eriococcus*	*Nymphanthus*
D1	*Phyllanthus* subgenus *Tenellanthus*	*Moeroris* subgenus *Tenellanthus*
D3	*Phyllanthus* subgenus *Swartziani*	*Moeroris* subgenus *Swartziani*
D4	*Phyllanthus* subgenus *Afroswartziani*	*Moeroris* subgenus *Moeroris*
E2	*Phyllanthus* subgenus *Conami*	*Phyllanthus* subgenus *Conami*
E4	*Phyllanthus* subgenus *Phyllanthus*	*Phyllanthus* subgenus *Phyllanthus*
E5	*Phyllanthus* subgenus *Xylophylla*	*Phyllanthus* subgenus *Xylophylla*
F1	*Phyllanthus* subgenus *Anesonemoides*	*Cicca* subgenus *Anesonemoides*
F1	*Phyllanthus* subgenus *Pseudogomphidium*	*Cicca* subgenus *Menarda*
F1	*Phyllanthus* section *Cicca*, *Polyanthi* & *Omphaocodopsis*	*Cicca* subgenus *Cicca*
F1	*Phyllanthus* subgenus *Betsileani*	*Cicca* subgenus *Betsileani*
F2	*Phyllanthus* subgenus *Gomphidium*	*Dendrophyllanthus*
G	*Phyllanthus* subgenus *Emblica*	*Emblica*
H	*Phyllanthus* subgenus *Phyllanthodendron*	*Glochidion subgenus Phyllanthodendron*
H	*Glochidion*	*Glochidion*
I	*Synostemon*	*Synostemon*
J	*Breynia*	*Breynia*

previous studies; (2) to analyse the historical biogeography of the genera in tribe Phyllantheae that made up *Phyllanthus* s.l.; and (3) to explain the speciation-distribution of the various clades and to assess the evidence for of pollinator related diversification.

Materials and methods

Sampling of tribe Phyllantheae

In this study we used a subset of the datasets employed in Bouman et al. (2021), which presents the largest sampling of *Phyllanthus* s.l. to date. To limit the extent and possible effects of missing data, we used the reduced dataset where we had genetic information for each accession with a minimum of 3500 nucleotides out of 5500. Species present with multiple samples in Bouman et al. (2021) are here limited to include only one accession, except for the *P. virgatus* complex where samples of Australia were retrieved in a different clade from those in Asia (presumed here to be *P. simplex*). The trimmed dataset contains 21 species of *Breynia*, four species of *Synostemon*, five species of *Glochidion*, four species of *Margaritaria* L.f., one species of *Flueggea* Willd. and 173 species of *Phyllanthus* s.l. *Leptopus chinensis* (Bunge) Pojark. and *Notoleptopus decaisnei* (Benth.) Vorontsova & Petra Hoffm. of tribe Poranthereae were used as an outgroup for tribe Phyllantheae. Almost all genera of the tribe were included except *Heterosavia* (Urb.) Petra Hoffm. and *Lingelsheimia* Pax as we did not have the full set of markers for any species from these genera. The sampling for *Phyllanthus* s.l. covers all reinstated genera (Table 9-1), the majority of sections and most of its distribution. Some geographical areas like India and the Neotropics are not well represented in this dataset and should be expanded upon in future studies.

Dating

A two-step approach was implemented to date the molecular phylogeny of *Phyllanthus*. In the first step, the molecular dataset presented by Kathriarachchi et al. (2005) and dated by Kawakita & Kato (2009) was re-calibrated with one additional fossil calibration point (see below) to obtain a base for the divergence time between tribe Phyllantheae and tribe Poranthereae (see supplementary table 9-1 for Genbank numbers). Outgroups were taken from the closest related family, the sister family Picrodendraceae (Xi et al. 2012). The dataset of Kathriarachchi et al. (2005) used the molecular markers *PHYC*, *atpb*, *matK* and *ndhF* and we therefore did not combine this with the dataset of Bouman et al. (2020), which consists of the molecular markers ITS, *PHYC*, *accD-psaI*, *matK* and *trnS-trnG*. In the second step, we implemented the divergence time between tribe Phyllantheae and tribe Poranthereae as a secondary calibration as indicated by the phylogeny of the Phyllanthaceae (Supplementary figure S9-1).

The molecular phylogeny of tribe Phyllantheae was dated using BEAST v. 1.10.4 (Suchard et al. 2018). The input file was prepared using BEAUTI v. 1.10.4

(within the BEAST package). MrModeltest v.2 (Nylander 2004) was used to obtain the best-fitting model according to the lowest Akaike Information Criterion (AIC) for each marker, selecting the same model for all markers. Substitution rates were calculated under the General Time Reversal (GTR) model with a discrete Gamma distribution (Γ, 4 categories of evolutionary rates among sites and a certain number of invariable sites (+I). Divergence times were estimated using an uncorrelated relaxed clock model (Drummond et al. 2007) with an exponential distribution of rates and the Yule process was selected as a tree prior (Yule 1925; Gernhard 2008) and a random starting tree was used. Two independent runs were done, each with 220 million generations of Markov Chain Monte Carlo (MCMC) and trees were sampled every 22,000 generations. Effective Sampling Sizes (ESS), representing the convergence of the two runs, were checked in Tracer v. 1.7.1 (Rambaut & Drummond 2018), while the Maximum Clade Credibility (MCC) tree for each run was checked for topological differences before combining the tree files using Logcombiner v.1.10.4 (part of the BEAST package) with a burnin of 20 % per tree file. TreeAnnotator v.1.10.4 (within the BEAST package) was used to find the MCC tree and this was visualized using Figtree v.1.4.3 (Rambaut 2014). Our analyses of divergence times were estimated using several fossils as calibration points. These were set as priors for specific taxon groups with an exponential distribution:

1. An Early Eocene calibration with a median age of 52.2 MA was put as offset for the prior with an exponential distribution and a mean of 1.5 to allow for older ages for the clade comprising *Flueggea* and *Phyllanthus* s.l. including *Glochidion*, *Breynia* and *Synostemon*. Fossil 3-colporate pollen of the Early Eocene (c. 47–56 Ma) Woolwich bed in Kent, England, was determined to be related to *Flueggea* or *Phyllanthus* (Gruas-Cavagnetto & Köhler 1992; Sagun & van der Ham 2003). Additional findings of *Flueggea*-type pollen from London (also Woolwich formation) and the Knopffeld formation in Austria from the Early Eocene (Hofmann et al. 2015) provided further support for this calibration point. The Woolwich bed finding has been used as a calibration point by Kawakita & Kato (2009), Luo et al. (2011b) and van Welzen et al. (2015). Older fruits from the Late Maastrichtian (66–72) Ma of India have been suggested to be related to the genus *Phyllanthus*, but could not be assigned with full certainty as fruits are notoriously difficult and there was no exhaustive comparison with fruits of other genera within the Phyllanthaceae family (Kapgate et al. 2017). Therefore we have opted to not include this in our analysis.
2. Leaf impressions tentatively assigned to *Glochidion* from the Middle Miocene (c. 11.6 Ma with a mean of 1.5) of India (Prasad 1994; Antal & Prassad 1996) were used as an offset minimum age constraint for Clade H, which contains *Glochidion* (also used in Kawakita & Kato 2009).
3. Recent findings of pantoporate pollen from the Changchang Formation

(Hainan Island, South China) have been attributed to *Phyllanthus* s.l. (Hofmann et al. 2019). The material is estimated to be of late Early Eocene (Bartonian, 37.8–48 Ma; Aleksandrova et al. 2015). This specific pollen type can be found in *Nymphanthus* Lour. (*Phyllanthus* subgenus *Eriococcus*) and subgenus *Ceramanthus* (listed as subgenus *Isocladus* section *Ceramanthus* in Hofmann et al. 2019, here listed in table 9-1 as *Cathetus* Lour.), but pollen sizes were more similar to those found in the latter. Therefore, this was used as an offset fossil calibration point for the clade comprising the sister groups *Phyllanthus* subgenus *Ceramanthus* and subgenus *Macraea* (*Cathetus*, Fig. 9-2; clade B) and the offset was set to 37.8 Ma with a mean of 1.5.

4. The stem age for the analysis of our dataset of tribe Phyllantheae was calibrated using divergence time estimates with tribe Poranthereae and Wielandieae taken from our analysis of the Phyllanthaceae family dataset and compared to Kawakita et al. (2009). The node was calibrated using an offset of c. 75 Ma with a mean of 1.5 to allow for older ages (see supplementary Fig. 9-1)

Additionally, to date the family Phyllanthaceae other calibration points similar to those implemented in Kawakita & Kato (2009) were implemented as an offset.

5. *Bischofia* pollen from the Middle Eocene (37.2–41.2 Ma) also from the

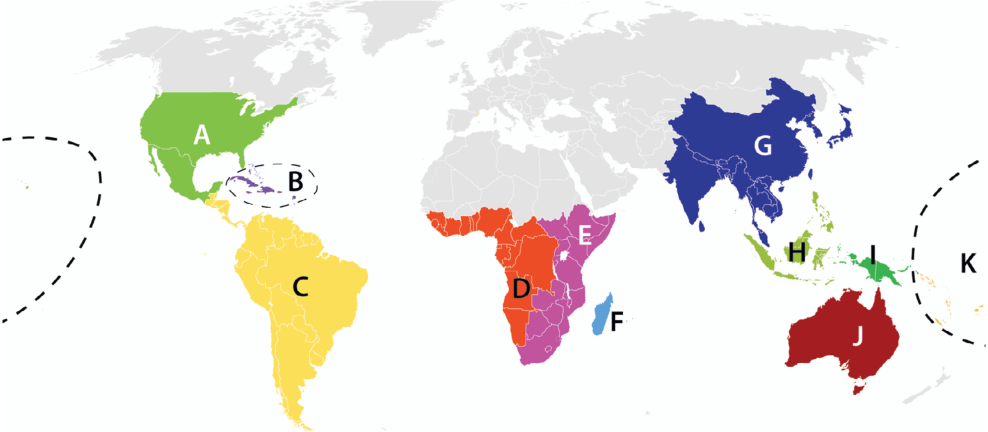


Figure 9-1. Map with biogeographical regions as specified for this study of Tribe Phyllantheae: A, North America to Mexico; B, West Indies; C, South America and part of the Panama Isthmus; D, West Africa with eastern border following Namibia, Democratic Republic of Congo and Central African Republic; E, South and Eastern Africa; F, Madagascar and the Mascarene Islands; G, mainland Asia stretching from India to Peninsular Malaysia; H, W. Malesia including Philippines; I, E. Malesia (mainly Papua New Guinea); J, Australia; K, Pacific Islands.

Woolwich formation in England was used as a minimum age constraint for the subfamily Antidesmatoidea (Gruas-Cavagnetto & Köhler 1992 as implemented in Kawakita & Kato 2009).

6. The clade containing tribe Poranthereae and tribe Wielandieae (sensu Hoffmann et al. 2006) was constrained with a calibration point based on *Actephila* Blume pollen type from the Late Eocene (median 33.9 Ma) of France (Gruas-Cavagnetto & Köhler 1992 as implemented in Kawakita & Kato 2009).
7. The stem age for the split between Phyllanthaceae and Picrodendraceae was conservatively set to 80 Ma based on molecular dating from Xi et al. (2012). Similar age estimates, but with varying 95% Highest Posterior Density (HPD) intervals have been obtained by Magallon et al. (2015), Davis et al. (2005) and Li et al. (2019). Kawakita & Kato (2009) opted to use the occurrence of Eudicot pollen as the root age for their phylogeny. As this is unlikely, since Phyllanthaceae occurred later, we decided to use the base estimate from the former papers.

Ancestral range estimation

Eleven biogeographical areas were specified based on levels of species endemism and tectonic history (Fig. 9-1). Distributions of the various species were taken from various monographs and floras (e.g. Webster 1956, 1957, 1958; Airy Shaw 1975, 1980; Bouman et al. 2018). The biogeographic area that covers islands in the Pacific Ocean covers mostly New Caledonia with over 100 endemic species of Dendrophyllanthus S.Moore (*Phyllanthus* subgenus *Gomphidium*). However, to not create separate areas for other islands, we also include islands from the rest of the Pacific. Most discussions below focus on New Caledonia unless specified otherwise.

The MCC tree resulting from our BEAST analysis was trimmed by excluding the outgroups of tribe Phyllantheae. Ancestral Range estimations were performed using RASP (Reconstructed Ancestral State in Phylogenies) 4.2 (Yu et al. 2015, 2020). We tested for different models for biogeographic inferences using the R package 'BioGeoBears' as implemented in RASP (Matzke 2013a, 2014). These were the S-Diva model (called Divalike in 'BioGeoBears'), DEC and BAYAREA (BAYAREALIKE), which is based on the likelihood of a given history and takes into account the relative probability of each biogeographic change and waiting times between events in a Bayesian framework (Landis et al. 2013). With the S-Diva model, the frequencies of ancestral ranges of specific nodes is averaged over all trees while alternative ranges are weighted by their frequency and node occurrence (Yu et al. 2010). 'BioGeoBears' additionally tests whether these models show a different/better fit when the founder effect (+J) is taken into account (Matzke 2013b, 2014). Usage of the founder effect as implemented by 'BioGeoBears' has recently been cautioned by Ree & Sanmartín (2018).

Dispersal constraints were defined for four time periods based on the geological history of the various continents involved. Dispersal constraints were defined similarly to those implemented by Buerki et al. (2011), Wei et al. (2015) and Thomas et al. (2015). These were mostly defined based on distance, but had a correction for specific land bridges and were categorized as very low dispersal = 0.01; low dispersal = 0.25; medium dispersal = 0.5; moderate dispersal = 0.75; high dispersal and adjacent areas = 1.0 (see Supplementary table 9-2). We allowed for 2–3 areas per node, as higher numbers gave far longer computation times with more ambiguous results. The model selection from BioGeobears, retrieved the highest Akaike Information Criterion (AIC) and weighted AIC score for the BAYAREALIKE model and DEC model (Table 9-2). BiogeoBears is able to compare the various models, but also incorporates a possible founder effect (+J). A likelihood Ratio test (LRT) was used to see if incorporating the founder effect gives a significantly different result. Table 9-2 shows a significant ($P < 0.05$) result for the comparisons DEC/DEC+J and BAYAREALIKE/BAYAREALIKE+J. The null hypothesis that the standard model and the model+founder effect show similar likelihoods for our data is therefore rejected and the analysis including the founder effect is omitted here as it has a lower AIC score.

Estimating and comparing speciation rates and identifying shift rates

To determine whether diversification rates differed per clade and could be associated with any specific ecological variable, we used BAMM v. 2.5 (Rabosky 2014) and the R package BAMMtools v. 2.1 (Rabovsky et al. 2014). In this method different models are fitted to the MCC tree to explore shifts in diversification rates. Speciation rates were calculated on the trimmed MCC tree and priors were adjusted to the scaling of our trees by using the command "setBAMMpriors". Differences in sampling number were adjusted for each clade according to the estimated number of species per subgenus (corrected with latest taxonomic findings sensu Bouman et al. 2020; Falcón et al. 2020). Rounded global sampling fractions for each clade were: *Nellica* Raf. 20%, *Cathetus* Lour. 40%, *Kirganelia* A.Juss. 54%, *Nymphanthus* 20%, *Lysiandra* ((F.Muell.) R.W.Bouman, I.Telford & J.J.Bruhl 41%, *Moeroris* Raf. 20 %, *Phyllanthus* s.s., the Neotropical clade 30%, *Dendrophyllanthus* 10%, *Cicca* 44%, *Emblica* 23%, *G.* subgenus *Phyllanthodendron* ((Hemsl.) R.W.Bouman) and *Glochidion* subgenus *Pseudoactephila* (Croizat) R.W.Bouman 10%, *Glochidion* 1.4%, *Synostemon* 10% and *Breynia* 25% (see table 9-1 for names under *Phyllanthus* s.l.). Initial runs indicated high speciation rates for *Glochidion*, so additional analyses were run with sampling of *Glochidion* set to 5% and 10% to compare overshadowing of signals. The MCMC was run for 10,000,000 generations and was saved every 1000 generations. Expected number of shifts was set to 3. A burn-in of 10% was discarded and Effective Sampling Sizes (ESS) were determined by using the Coda Package for R (Plummer et al. 2006). The output was further analysed using BAMMtools to determine the single best shift configuration and the maximum shift credibility configuration. Independent speciation rates for the various clades (Fig.

Table 9-2. Model comparison from BioGeoBears showing lognormal likelihood (LnL), Akaike Information Criterion (AIC) and weighted AIC (AICwt) and comparison to incorporation of founder effect. Founder effect is tested using the Likelihood Ratio Test.

	LnL	**numparams**	**d**	**e**	**j**	**AICc**	**AICc_wt**	**LRT test**
DEC	-428,7	2	0,0052	1,00E-12	0	861,5	7,70E-11	
DEC+J	-408,8	3	0,0035	1,00E-12	0,02	823,7	0,013	2,60E-10
DIVALIKE	-425,2	2	0,0059	1,00E-12	0	854,5	2,60E-09	
DIVALIKE+J	-415	3	0,0042	1,00E-12	0,015	836,1	2,50E-05	6,30E-06
BAYAREALIKE	-483,1	2	0,004	0,034	0	970,2	2,00E-34	
BAYAREALIKE+J	-404,4	3	0,0021	0,004	0,025	815	0,99	4,50E-36

9-2: clades A–J while separating C1, C3, C4, F1 & F2) were also extracted in R.

Results

Divergence time estimation

Our reconstruction of *Phyllanthus* s.l. and related genera indicate that the clade originated sometime during the Late Paleocene or Early Eocene. The MCC tree resulting from BEAST for the Phyllanthaceae had generally high node support (Supplementary Fig. 9-1). Node support was only a bit lower within a few genera and within the subfamily Antidesmatoideae between genera (PP>0.74). Despite differing constraints on the divergence node between Picrodendraceae and Phyllanthaceae, both family-level analyses resulted in an estimated age for the divergence between tribe Phyllantheae with tribe Wielandieae and Porantthereae around 75 Ma (HPD 94–63 MA; Supplementary Fig. 9-1). This resulted in our setting of 75 as a median age for the stem age of our analysis of *Phyllanthus* s.l. and the other genera.

The phylogeny focusing on *Phyllanthus* s.l. and related genera showed no major topological differences with previous analyses (Fig. 9-2). Additional age estimations in BEAST while excluding the calibration point for the genus *Glochidion* (based on Prasad 1994; Antal & Prassad 1996), did not result in significant changes to age estimations of this (12.41 Ma; Table 9-3) and other clades. Placing the fossil calibration point of pantoporate pollen (Aleksandrova et al. 2015) as the crown age of *Nymphanthus* instead of *Cathetus* resulted in slightly older nodes for the outgroups, *Nellica* (Clade A) and *Cathetus* (Clade B), but with lower ESS scores. The crown age of tribe Phyllantheae was dated to c. 60 Ma (HPD 53.45–72.38 Ma) (Fig. 9-2). The crown age of Clade C, which corresponds here to *Kirganelia*, *Nymphanthus* and the Australian "*Lysiandra* clade" is estimated to be around 36 Ma (HPD 28.83–45.08). Similarly the crown age of Clade D ("large African" clade) and Clade E (Neotropical clade) are 34.44 Ma (HPD 27.30–41.87) and 32.01 Ma (HPD 24.65–39.34), respectively. Clade F can be divided into two major taxonomical subclades: F1 which corresponds to *Dendrophyllanthus*; F2 which corresponds to the reinstated genus *Cicca* L., which contains several sections and subgenera from *Phyllanthus* s.l. (Table 9-1). Clade F1 includes species from a multitude of areas and the crown age is estimated to be 27.69 Ma (HPD 19.71–35.76). The crown age of *Emblica* (node G) was inferred to be 18.7 Ma (HPD 10.98–26.50). The genera *Glochidion* (including *P.* subgenus *Phyllanthodendron*), *Breynia* and *Synostemon* are estimated to have diverged from other species of *Phyllanthus* s.l. in the Late Oligocene/Early Miocene at 26.24 Ma (HPD 19.34–38.44).

Ancestral area estimation

Node 1 and 2 (Fig. 9-2) were omitted from the biogeographic analysis as outgroups were removed. While nodes 9–11 show medium support for an ancestral area in mainland Asia, support for nodes 3–8 is generally low and could only infer a wide ancestral area for *Phyllanthus* s.l. Node 3 (common ancestor of *Phyllanthus* s.l. + *Glochidion* + *Breynia* + *Synostemon*) was inferred to be Africa, Mainland Asia or Australia by BAYAREA (PP 0.33) while DEC indicated a wider area of North America, Eastern Africa and mainland Asia (Relative Probability 0.33).

The ancestral area of Clade A was reconstructed to be in North America or Africa (PP = 0.20, RP =0.35; Fig. 9-2). Both BAYAREALIKE and DEC indicate an ancestral area of Africa to Asia for *Cathetus* (*P.* subgenus *Cathetus* and *Macraea*, Clades B1 & B2; Fig. 9-2). Both subclades in this group show dispersal exchanges between Africa and Asia, but only *C.* subgenus *Macraea* has species present in Australia.

Clade C (Fig. 9-2) consists of three major clades, which correspond respectively to *Kirganelia* (C1); *Lysiandra* (C3) and *Nymphanthus* (C4). While BAYAREALIKE reconstructed the area to be quite wide, ranging from West Africa to Asia (PP = 0.51), DEC indicated an African origin (C1 RP = 0.56) with two separate instances of dispersal events to Asia. One dispersal and speciation event into Madagascar is found in *Kirganelia* in both analyses. *Lysiandra* consists of species occurring only in Australia, which is consistent with a single dispersal and subsequent speciation event found for node C3 (PP = 0.72, RP = 1). *Nymphanthus* is inferred to have originated in mainland Asia (C4 PP = 0.45, RP = 0.73) with two independent dispersals to Malesia and further.

The ancestral area of *Moeroris* (*P.* subgenus *Tenellanthus*, *Swartziani* and *Afroswartziani*, Clade D) is estimated to be in Africa (BAYAREALIKE: DE, PP = 0.46; DEC: D, RP = 0.39; Fig. 9-2). The majority of species are distributed in Africa, but we find one dispersal event to North America (*M. aranaria* (A.Gray) R.W.Bouman) and one to South America (*Moeroris stipulata* Rafinesque) and dispersal event to Madagascar (Fig. 9-2).

The large Neotropical clade (E), consisting of *Phyllanthus* subgenus *Phyllanthus*, *Conami* (Aubl.) G.L.Webster and *Xylophylla* (L.) Pers., is inferred to have originated in South America (node E, PP = 0.27; DEC: AC, RP = 0.98; Fig. 9-2). Some species of *P.* subgenus *Phyllanthus* are currently found in North America. Within subgenus *Xylophylla* we find an exchange between South America and the Carribean, but we were unable to reconstruct the ancestral area for this.

The ancestral area of the speciose genus *Dendrophyllanthus* (F2) is inferred to be Australia (PP = 0.65, RP = 0.74) and it gave rise to independent dispersals to New Caledonia in both subclades (Fig. 9-2). One clade contains two independent dispersals from Australia to Papua New Guinea. The ancestral area of *Cicca* (F1) is inferred to be in Madagascar with one lineage (*corresponding to C.* subgenus *Cicca*) subsequently dispersing to Africa and South America.

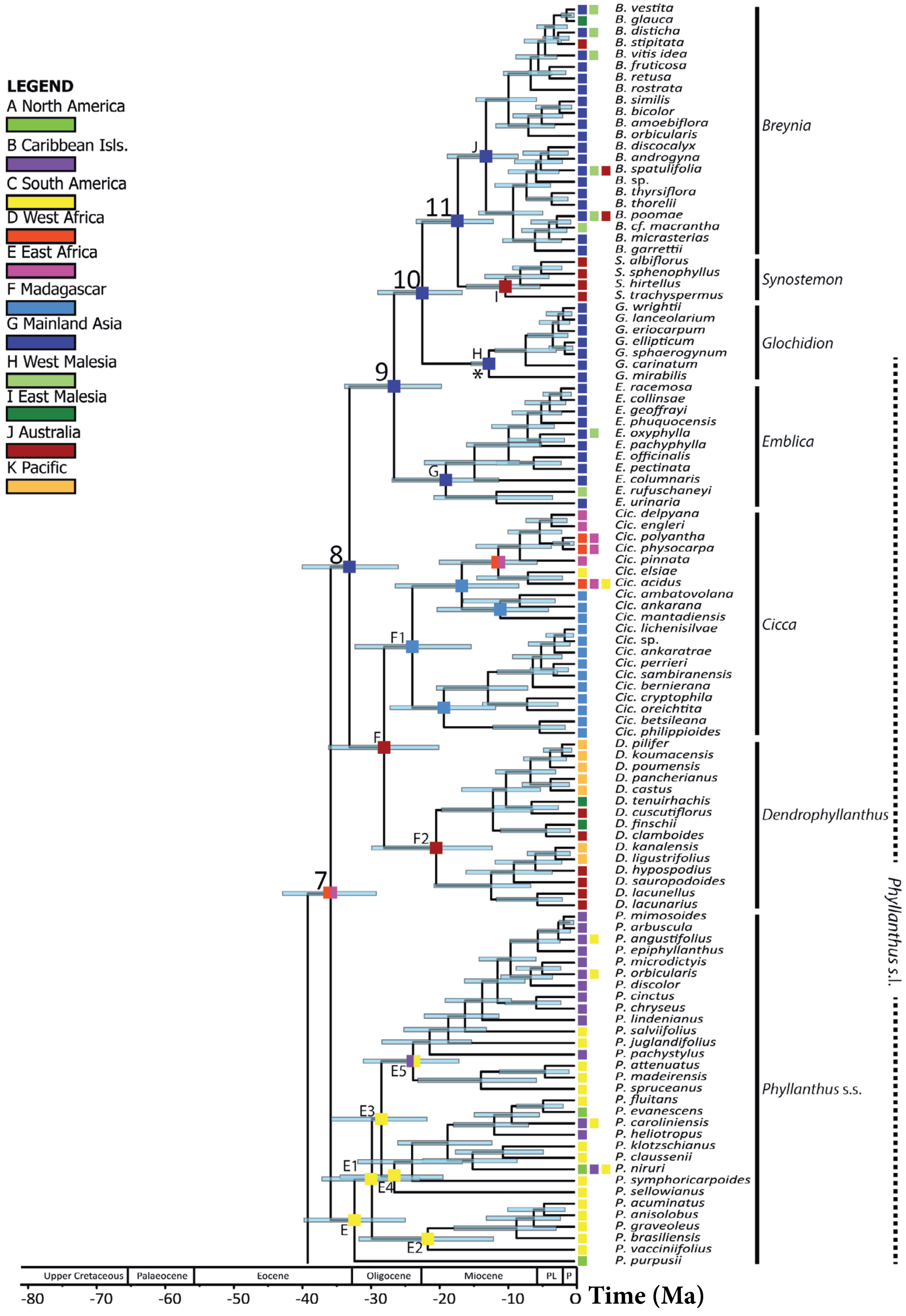
Emblica (G), and the genera *Glochidion* (H), *Synostemon* (I) and *Breynia* (J), were reconstructed to have an ancestral area in mainland Asia, with for *Synostemon* a single dispersal event to Australia.

Table 9-3. Summary of the dated phylogeny and ancestral area reconstruction for major clade nodes following figure 9-2. Shown are for each major node node the posterior probabilities, mean ages of the nodes, 95% height of the Posterior Density intervals, BAYAREA reconstruction with next to it the Posterior Probability and DEC with relative probability.

Node label	Posterior	Age	95% HPD	Bayarea	PP	DEC	RP
1	0,58	60,51	72.38-53.45				
2	1	55,11	61.36-53.00				
3	0,98	51,79	58.36-46.00	DGJ	0,3255	AEG	0,3286
4	1	48,74	55.09-42.78	DGJ	0,3369	G	0,4675
5	1	44,64	51.24-38.17	DGJ	0,3247	G	0,2325
6	1	38,84	45.54-32.22	DEG	0,2293	A	0,1134
7	0,99	35,48	42.47-28.86	DG	0,1774	ACJ	0,1453
8	0,91	32,75	39.62-25.66	G	0,2281	J	0,4717
9	1	26,24	33.44-19.34	G	0,6	G	0,9155
10	1	22,13	28.59-16.32	G	0,6576	G	0,5304
11	1	16,95	22.99-11.80	G	0,5834	GJ	0,7594
A	1	22,66	41.25-9.05	AE	0,2049	AEG	0,3526
B	1	38,17	41.16-37.20	DG	0,3682	G	0,3432
B1	1	25,72	34.27-17.14	DG	0,5034	DG	0,9719
B2	1	13,5	25.58-5.32	DG	0,7446	DG	1
C	1	36,84	45.08-28.83	DGJ	31,02	G	0,5763
C1	1	21,24	36.01-9.87	DG	0,5147	D	0,5557
C2	1	29,58	38.12-21.93	G	0,3519	GJ	0,5531
C3	1	23,62	31.62-15.72	J	0,7152	J	1
C4	1	23,74	31.88-16.28	G	0,451	G	0,7299
D	1	34,44	41.87-27.30	DE	0,4641	D	0,3933
D1	1	21,32	33.45-10.24	DE	0,7973	D	0,4275
D2	0,95	31,7	39.06-24.56	DE	0,6249	AD	0,2895
D3	1	19,83	30.83-9.81	DE	0,7246	AD	0,4768
D4	1	27,4	34.32-21.07	DE	0,8499	E	0,6935
E	0,99	32,01	39.34-24.63	C	0,2731	AC	0,9773
E1	1	29,48	36.74-22.50	C	0,4156	C	0,9867
E2	0,57	21,32	31.34-11.75	C	0,6525	C	0,6188
E3	0,4	28,09	35.38-21.46	C	0,3893	C	0,7495
E4	0,47	26,21	34.10-19.12	C	0,3853	C	0,9812

E5	1	23,47	30.72-16.81	BC	0,5265	BC	0,9842
F	0,66	27,69	35.76-19.72	J	0,1184	FJ	0,7084
F1	1	23,58	31.92-15.02	F	0,5128	F	0,6396
F2	1	20,11	29.49-11.96	J	0,6532	J	0,7425
G	1	18,7	26.42-10.98	GH	0,8815	GH	0,6422
H	1	12,41	14.10-11.60	G	0,9435	G	1
I	1	12,84	18.48-8.17	G	0,965	G	0,9924
J	1	10,02	15.70-4.98	J	0,8953	J	1

Figure 9-2. Chronogram (MCC tree) of tribe Phyllantheae generated via Bayesian analysis in BEAST. Axis scaled to node ages and with designated time periods according to International Commission on Stratigraphy (ICS) V. 2020/03. Calibration points are indicated with *, major nodes are numbered 1–11 while clades follow A–J as discussed in text. Ancestral area estimation as inferred from the BAYAREALIKE model from BiogeoBears given for selected nodes in squares with legend for the different areas, colours correspond to map of figure 1. A broader definition of *Phyllanthus* from previous classifications is shown with a dotted line on the right. Figure shown on following two pages


LEGEND
A North America
B Caribbean Isls.
C South America
D West Africa
E East Africa
F Madagascar
G Mainland Asia
H West Malesia
I East Malesia
J Australia
K Pacific
B. vestita
B. glauca
B. disticha
B. stipitata
B. vitis idea
B. fruticosa
B. retusa
B. rostrata
B. similis
B. bicolor
B. amoebiflora
B. orbicularis
B. discocalyx
B. androgyna
B. spatulifolia
B. sp.
B. thyrsiflora
B. thorelii
B. poomae
B. cf. macrantha
B. micrasterias
B. garrettii
S. albiflorus
S. sphenophyllus
S. hirtellus
S. trachyspermus
G. wrightii
G. lanceolarium
G. eriocarpum
G. ellipticum
G. sphaerogynum
G. carinatum
G. mirabilis
E. racemosa
E. collinsae
E. geoffrayi
E. phuquocensis
E. oxyphylla
E. pachyphylla
E. officinalis
E. pectinata
E. columnaris
E. rufuschaneyi
E. urinaria
Cic. delpyana
Cic. engleri
Cic. polyantha
Cic. physocarpa
Cic. pinnata
Cic. elsiae
Cic. acidus
Cic. ambatovolana
Cic. ankarana
Cic. mantadiensis
Cic. lichenisilvae
Cic. sp.
Cic. ankaratrae
Cic. perrieri
Cic. sambiranensis
Cic. bernierana
Cic. cryptophila
Cic. oreichtita
Cic. betsileana
Cic. philippioides
D. pilifer
D. koumacensis
D. poumensis
D. pancherianus
D. castus
D. tenuirhachis
D. cuscutiflorus
D. finschii
D. clamboides
D. kanalensis
D. ligustrifolius
D. hypospodius
D. sauropodoides
D. lacunellus
D. lacunarius
P. mimosoides
P. arbuscula
P. angustifolius
P. epiphyllanthus
P. microdictyis
P. orbicularis
P. discolor
P. cinctus
P. chryseus
P. lindenianus
P. salviifolius
P. juglandifolius
P. pachystylus
P. attenuatus
P. madeirensis
P. spruceanus
P. fluitans
P. evanescens
P. caroliniensis
P. heliotropus
P. klotzschianus
P. claussenii
P. niruri
P. symphoricarpoides
P. sellowianus
P. acuminatus
P. anisolobus
P. graveoleus
P. brasiliensis
P. vacciniifolius
P. purpusii
Breynia
Synostemon
Glochidion
Emblica
Cicca
Dendrophyllanthus
Phyllanthus s.s.
Phyllanthus s.l.
J
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I
10
H
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9
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F1
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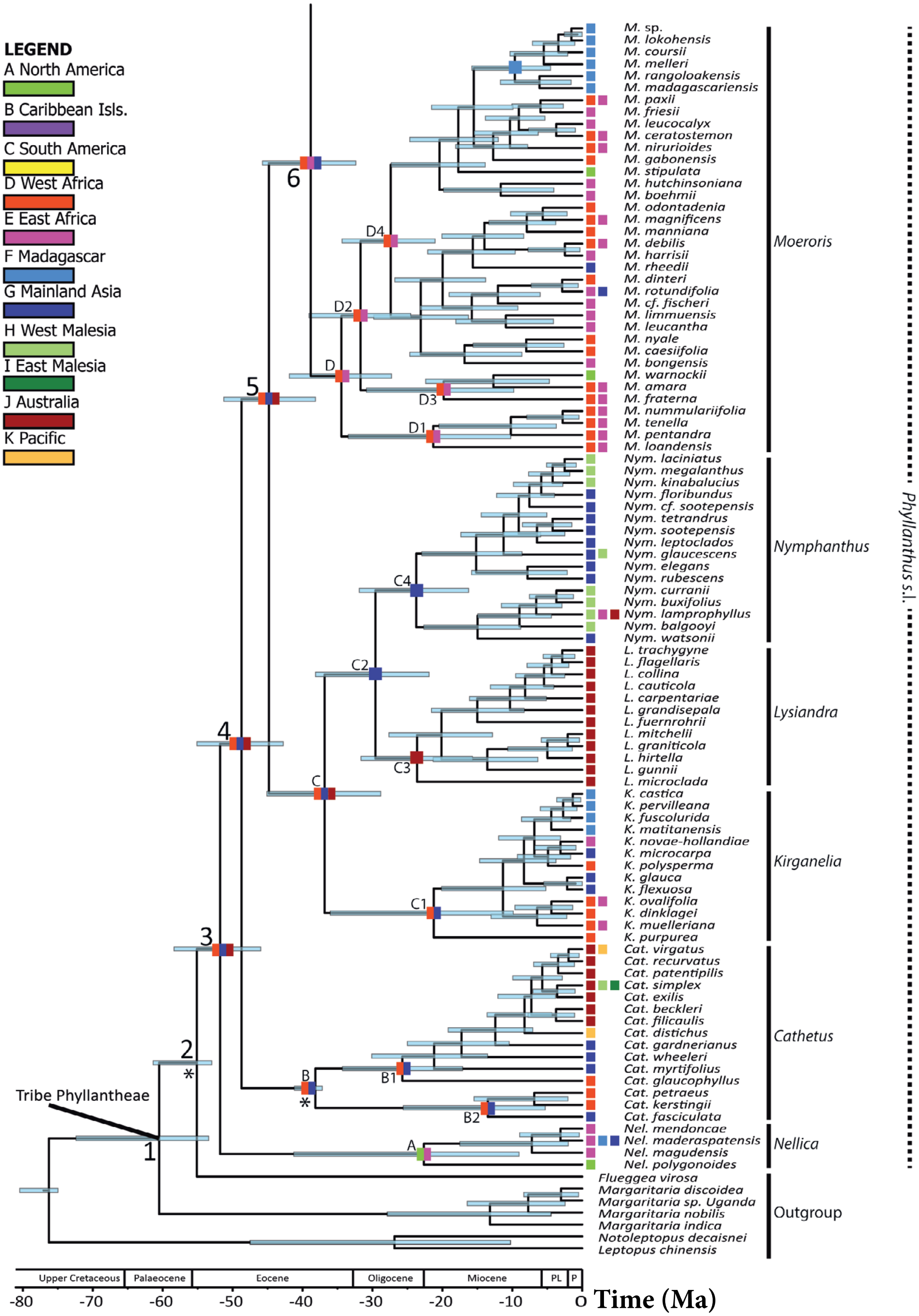
F2
7
E5
E3
E1
E4
E
E2
Upper Cretaceous
Palaeocene
Eocene
Oligocene
Miocene
PL
P
-80
-70
-60
-50
-40
-30
-20
-10
0
Time (Ma)


LEGEND
A North America
B Caribbean Isls.
C South America
D West Africa
E East Africa
F Madagascar
G Mainland Asia
H West Malesia
I East Malesia
J Australia
K Pacific
Tribe Phyllantheae
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C4
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D2
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D4
M. sp.
M. lokohensis
M. coursii
M. melleri
M. rangoloakensis
M. madagascariensis
M. paxii
M. friesii
M. leucocalyx
M. ceratostemon
M. nirurioides
M. gabonensis
M. stipulata
M. hutchinsoniana
M. boehmii
M. odontadenia
M. magnificens
M. manniana
M. debilis
M. harrisii
M. rheedii
M. dinteri
M. rotundifolia
M. cf. fischeri
M. limmuensis
M. leucantha
M. nyale
M. caesiifolia
M. bongensis
M. warnockii
M. amara
M. fraterna
M. nummulariifolia
M. tenella
M. pentandra
M. loandensis
Nym. laciniatus
Nym. megalanthus
Nym. kinabalucius
Nym. floribundus
Nym. cf. sootepensis
Nym. tetrandrus
Nym. sootepensis
Nym. leptoclados
Nym. glaucescens
Nym. elegans
Nym. rubescens
Nym. curranii
Nym. buxifolius
Nym. lamprophyllus
Nym. balgooyi
Nym. watsonii
L. trachygyne
L. flagellaris
L. collina
L. cauticola
L. carpentariae
L. grandisepala
L. fuernrohrii
L. mitchelii
L. graniticola
L. hirtella
L. gunnii
L. microclada
K. castica
K. pervilleana
K. fuscolurida
K. matitanensis
K. novae-hollandiae
K. microcarpa
K. polysperma
K. glauca
K. flexuosa
K. ovalifolia
K. dinklagei
K. muelleriana
K. purpurea
Cat. virgatus
Cat. recurvatus
Cat. patentipilis
Cat. simplex
Cat. exilis
Cat. beckleri
Cat. filicaulis
Cat. distichus
Cat. gardnerianus
Cat. wheeleri
Cat. myrtifolius
Cat. glaucophyllus
Cat. petraeus
Cat. kerstingii
Cat. fasciculata
Nel. mendoncae
Nel. maderaspatensis
Nel. magudensis
Nel. polygonoides
Flueggea virosa
Margaritaria discoidea
Margaritaria sp. Uganda
Margaritaria nobilis
Margaritaria indica
Notoleptopus decaisnei
Leptopus chinensis
Moeroris
Nymphanthus
Lysiandra
Kirganelia
Cathetus
Nellica
Outgroup
Phyllanthus s.l.
Upper Cretaceous
Palaeocene
Eocene
Oligocene
Miocene
PL
P
-80
-70
-60
-50
-40
-30
-20
-10
0
Time (Ma)

Diversification rate heterogeneity

Effective sample sizes after burnin were >600 for both the number of shifts and log likelihoods and MCMC chain convergence was confirmed. Speciation rates (λ) overall were 0.19 species/million years [95% interval 0.16–0.21] while mean extinction rates (μ) were 0.03 sp/Ma [95% interval 0.01–0.06]. Speciation rates were relatively similar between the clades of *Nellica* (Clade A) and the Neotropical Clade E at 0.15 species/Myr (Table 9-3). Extinction rates for these clades was relatively low at 0.01 species/Myr. An increase in speciation rates can be seen in Clades F–J, with highest speciation occurring in Clade H (*Glochidion*) at 0.56 species/Myr. The 95 % credible set of rate shift configurations sampled with BAMM included fifteen distinct shift configurations, mostly indicating a shift in speciation of the genus *Glochidion* (Fig. 9-3, clade H). This shift was also found by the Maximum shift credibility plot. Additional shift changes were found at node 8, which encompasses the clades with higher speciation as seen in Table 9-4. The rate-through-time plot of tribe Phyllantheae shows a steady increase from its inception, with a sudden increase in speciation rate around 10 Ma. Plots of *Kirganelia* (Clade C1) and *Cicca* (Clade F1) show a slight increase, but then decreasing of the curve. The genus *Dendrophyllanthus* (Clade F2) shows an increasing speciation rate through time, but not as drastic as observed for *Glochidion* (clade H), which is close to exponential. The rate through time plot of *Breynia* and *Synostemon* (supplementary figure 4) also show a rate higher than the mean speciation rate through time with a slight smoothing of the curve towards the present.

Discussion

Age estimates

Our reconstruction of *Phyllanthus* s.l. and related genera indicates that the clade originated sometime during the Late Paleocene or Early Eocene. The MCC tree resulting from BEAST for the Phyllanthaceae showed no major topological differences with the one presented by Kathriarachchi et al. (2005) and node support was generally high (Supplementary Fig. 1) The dated phylogeny is largely congruent with the results of previous studies (e.g. Kawakita & Kato 2009; Luo et al. 2011b; van Welzen et al. 2015), but provides a better supported backbone between the major clades of tribe Phyllantheae. The recent species-level dated phylogeny of angiosperms by Janssens et al. (2020) inferred that Angiosperms originated before the Cretaceous, which would indicate older ages for the major clades of flowering plants. Nevertheless, the crown age of tribe Phyllantheae is inferred in their study at 65.92 Ma (HPD 74.33–45.58; Janssens et al. 2020; derived from supplementary material 5), which is comparable to our results (60.51 Ma; HPD 72.38–53.45). Divergence times estimations of *Breynia* and *Synostemon* were comparable to those found in van Welzen et al. (2015). The crown age of *Breynia*, 12.84 Ma (Table 9-3; HPD 18.48–8.17) was found to be more recent than the reconstruction of van Welzen et al. (2015; 20.6 Ma), while *Glochidion* seemed older (12.41 Ma here vs 5.61

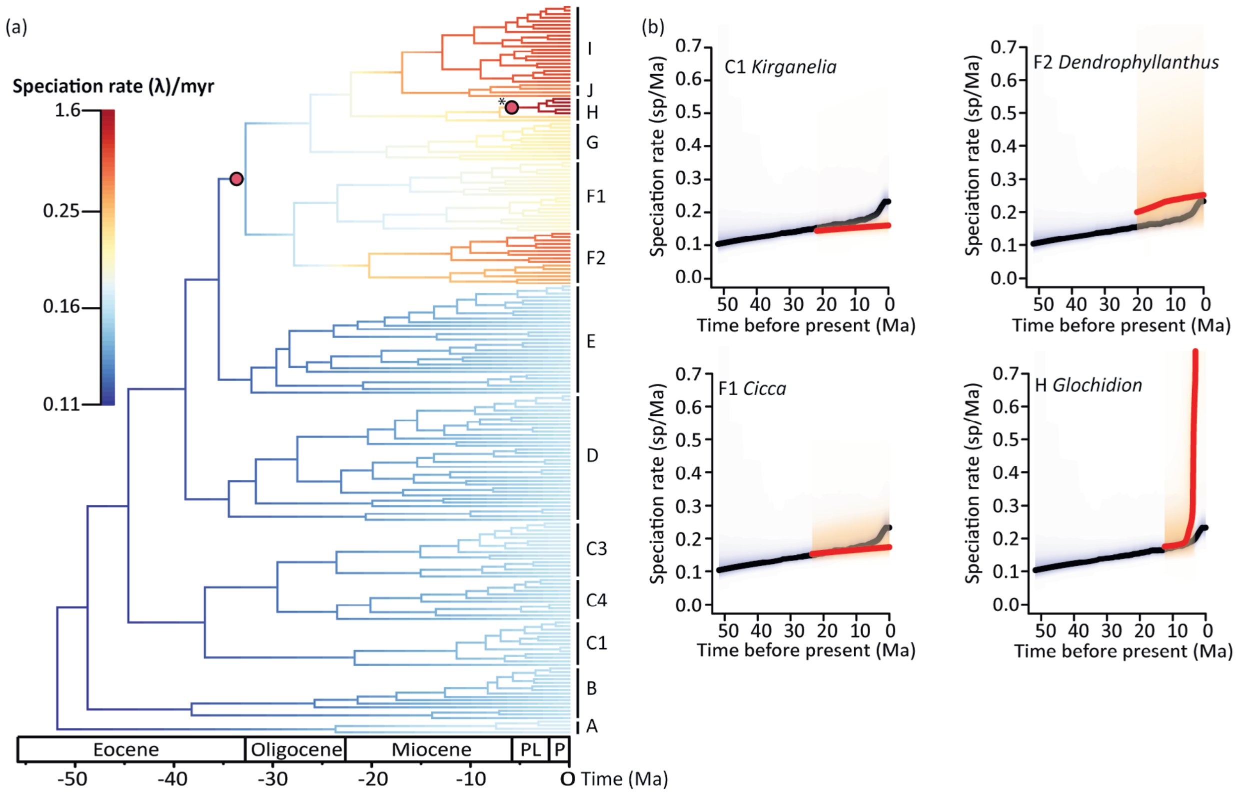


Figure 9-3. Speciation rate (λ) of *Phyllanthus*, *Glochidion*, *Bryenia* and *Synostemon*. (a) Chronogram of Phyllanthus with branch lengths colored according to speciation rate following Jenks bucketing. Red circles indicate shifts in speciation rates as found by the best credible shift analyses, asterisk (*) includes those found by maximum posterior shift probability. (b) Speciation rates through time of selected clades. Black line represents mean speciation rate through time of the whole phylogeny, red is of selected clade.

Table 9-4. Median speciation (λ), extinction (μ) and net diversification rates (with 95% CI) For *Glochidion*, *Breynia*, *Synostemon* and major clades within *Phyllanthus*. Clades as in Fig. 9-2.

		Speciation		Extinction		Net Diversification	
Clade	**Age**	**Median**	**95% CI**	**Median**	**95% CI**	**Median**	**95% CI**
All	51,79	0,18	0.16–0.21	0,02	0.01–0.06	0,16	0.15–0.16
A *Nellica*	22,66	0,15	0.12–0.19	0,01	0.001–0.10	0,13	0.09–0.12
B *Cathetus*	38,17	0,15	0.13–0.18	0,01	0.001–0.06	0,14	0.12–0.13
C1 *Kirganelia*	21,24	0,15	0.13–0.19	0,01	0.001–0.05	0,14	0.13–0.13
C2 *Lysiandra*	23,62	0,15	0.13–0.10	0,01	0.001–0.05	0,14	0.13–0.13
C4 *Nymphanthus*	23,74	0,16	0.13–0.19	0,01	0.001–0.06	0,14	0.14–0.13
D *Moeroris*	34,44	0,15	0.13–0.18	0,01	0.001–0.05	0,14	0.13–0.13
E *Phyllanthus* s.s.	32,01	0,15	0.13–0.18	0,01	0.001–0.05	0,14	0.13–0.13
F1 *Cicca*	23,58	0,17	0.14–0.28	0,01	0.001–0.06	0,16	0.21–0.14
F2 *Dendrophyllanthus*	20,11	0,24	0.15–0.56	0,02	0.001–0.34	0,22	0.21–0.15
G *Emblica*	18,7	0,17	0.14–0.30	0,01	0.001–0.08	0,16	0.22–0.14
H *Glochidion*	12,41	0,56	0.40–0.75	0,07	0.01–0.24	0,50	0.51–0.39
I *Breynia*	12,84	0,30	0.17–0.49	0,03	0.002–0.24	0,26	0.27–0.17
J *Synostemon*	10,02	0,27	0.16–0.47	0,03	0.002–0.24	0,24	0.26–0.15

Ma in van Welzen et al. 2015). This is not entirely explained by the fossil calibration point for *Glochidion*, as additional analyses without this fossil gave similar results. More likely, it is caused by a combination of including more fossil calibration points as well as a larger sampling.

Origin of Phyllanthus and related genera

Fossil pollen indicates that several taxa of tribe Phyllantheae were already present in Europe during the early Eocene and pollen attributed here to Clade B (*Cathetus*) indicates an early dispersal to China (Gruas-Cavagnetto & Köhler 1992; Hofmann et al. 2015, 2019). The pantropical genus *Margaritaria* is reconstructed to have diversified during the Middle Miocene (Fig. 9-2), but it was not used in our reconstruction of the ancestral areas. The Asian species *M. indica* (Dalzell) Airy Shaw was previously retrieved as sister to the other species from South America and Africa (Webster 1979; Bouman et al. 2021). Fossil findings from the Eocene could indicate that boreotropic migration was part of the history of *Phyllanthus* s.l. and possibly *Flueggea* Willd. and that taxa later dispersed to Asia, Africa and North America while becoming extinct in Europe. The genus *Flueggea* might have persisted in Europe as *F. tinctoria* (L.) G.L.Webster is native to Spain and Portugal (Webster 1984), while there is only one invasive species of *Phyllanthus* (*P. tenellus* Roxb. to be placed in *Moeroris* Raf.) in Europe (Crisafulli et al. 2011). Limited sampling of *Nellica* and *Flueggea*, however, prevents us from further inferences; the European species *F. tinctoria* would be especially interesting to include in future studies. The major nodes 3–5 of the backbone phylogeny of *Phyllanthus* s.l. are reconstructed to have a wide ancestral area with an unclear area of origin (Fig. 9-2). Our reconstruction shows this wide ancestral area for the nodes in the time period just after the PETC till the start of the late Eocene (38.84 Ma; HPD 45.54–32.22, Table 9-3). Species of *Nellica* (Clade A) are found in North America, Africa and Asia, which is consistent with a boreotropic origin. However, the estimate for the crown age for Clade A (22.66 Ma; HPD 41.25–9.04) shows a wide margin, which could start in the Eocene, but also could be quite recent. Clade A needs to be further explored as not all species from India have been confidently assigned to this taxonomic group based on morphology (Bouman et al. 2018) and the connection with North America has only recently been confirmed for one species (Bouman et al. 2021). A higher sampling might give a better resolution when these species diverged and spread to different continents.

Our results confirm earlier studies (Kawakita & Kato 2009; Luo et al. 2011b), that tribe Phyllantheae probably diverged from other tribes after the breakup of Gondwana and the breakup of India and Madagascar at 90–85 Ma. The sampling from India in our study is sparse and could represent an interesting aim for future studies. Some species from Sri Lanka (*Cathetus gardnerianus* (Wight) R.W.Bouman and *Nymphanthus floribundus* (Wight) R.W.Bouman), are firmly nested in clades B and C and are found to be of more recent origins in the Miocene

(Fig. 9-2). The separation of India from Africa and Madagascar is reconstructed to have occurred in the Cretaceous (Ali & Aitchinson 2008; Hall 2012). The much later collision of India with the Asian plate probably occurred somewhere around 35 Ma (Ali & Aitchinson 2008) with a possible earlier connection with Malesia and Myanmar around 57 Ma (Aitchinson et al. 2007). The flora of India harbours species of several clades from tribe Phyllantheae, but not many from those found on Madagascar (see Bouman et al. 2018). The species included here seem to have diverged much more recently and do not support the Indian raft hypothesis for tribe Phyllantheae. However, an expanded sampling of for example the genera *Cathetus* and *Nellica* is necessary to further investigate the relationship of Indian taxa within the tribe.

Out of Africa

Many clades in tribe Phyllantheae contain species distributed in Africa, but unfortunately the major nodes between these groups show less resolution and are usually reconstructed with wide ancestral areas. Dispersals from Africa to other areas can still be inferred in a few clades. *Kirganelia* (Fig. 9-2, node C1) was reconstructed to have an ancestral area in Africa and Asia. *Kirganelia purpurea* (Müll.Arg.) R.W.Bouman and a clade containing several African species is found to be sister to a mixed clade of African, Asian and Malagasy species, which show several dispersal events in the Late Miocene.

Clade D, which consists of three subgenera in *Phyllanthus* in now transferred to the reinstated genus *Moeroris* Raf. (Bouman et al. 2022). This group was estimated to contain almost 200 species (Bouman et al. 2022), which are mostly distributed in Africa. A single dispersal event to Madagascar is found in Clade D during the Miocene and two independent dispersals are found to the Americas. *Moerorist stipulata* Raf. was included here as the only representative of a specific West Indian clade with some species also distributed in South America (see Falcón et al. 2020; Bouman et al. 2021) and it is reconstructed to have diverged from other African species around the Oligocene-Miocene transition. No land bridges are known between these continents at the time when they were much closer to their present day distribution, so this event was likely due to long-distance dispersal. Dispersal from Africa to Madagascar has been inferred to have been easier before a shift in ocean currents around 20–15 Ma (Samonds et al. 2012). Interestingly, the dispersal event within Clade D to Madagascar around the Mid-Miocene (C. 9.8 Ma, HPD 15.76–4.55) occurred either at the end or after this shift. Over-water dispersal could still occur, but was complicated and it is unclear how the species of *Moeroris* crossed this barrier as the capsular fruits are usually not eaten by other dispersal vectors such as birds.

Colonizing the Americas and West Indies

The large Neotropical clade of *Phyllanthus* s.s. (Clade E) seems to have arrived in South America during the Late Eocene-Oligocene (Fig. 9-2). Following our reconstruction, it diverged from an African ancestor (Fig. 9-2, node 7) at the end of the Eocene. Similar dispersal events were found in other taxa such as platyrrhine monkeys (Seiffert et al. 2020), Arecaceae (Cuenca et al. 2008) and the Clusioid clade of the Malpighiales (Ruhfel et al. 2016), which were attributed also to sea currents (Renner 2003) or a possible boreotropical origin. The majority of Neotropical species of *Phyllanthus*, but also those of the African Clade D, have schizocarpic fruits that self-disperse the seeds. Some observations have been made on how these seeds behave in water (Breteler, pers. comm.), but larger studies on dispersal in *Phyllanthus* have not been done. The ancestral area of Clade E was estimated to be the Neotropics, but *P. purpusii* Brandegee, which is sister to the other species of Clade E (Fig. 9-2; Bouman et al. 2021), is from Mexico. This indicates an early dispersal between North and South America at the formation of the Isthmus of Panama (Jaramillo 2018). Other dispersals to North America are difficult to reconstruct here due to sampling limitations as these are from more widespread species. There are some taxa like *P. pseudocicca* Griseb. and *P. subcarnosus* C.Wright ex Griseb. that were proposed to have arrived independently (Falcón et al. 2020), but their phylogenetic position could not be reconstructed with full certainty.

The *Phyllanthus* flora of the West Indies seems to have originated in the Neotropics and it reached the Carribean at the end of the Oligocene (*P. pachystylus* Urb.) or in the Miocene (majority of *P.* subgenus *Xylophylla*, Fig. 9-2, node E5). To explain the origin of the Caribbean flora, some authors have hypothesized that there was a land-bridge or island chain between South America and the Antilles at the Eocene-Oligocene boundary (Iturralde-Vinent & McPhee 1991). However, this connection was not found for taxa that seemingly originated in South America and dispersed after this period (Nieto-Blázquez et al. 2017). These results seem to be congruent with our findings, that *Phyllanthus* dispersed to the West Indies on several independent occasions, but after the Eocene. A higher sampling of the South American species of *Phyllanthus* could allow for a further scrutiny in dispersal areas between countries as the area is defined here rather wide.

East Malesia, Australia and the New Caledonian interchange

The main diversity of the more than 150 species of *Phyllanthus* subgenus *Gomphidium* is found today on the islands of New Caledonia and Papua New Guinea (Airy Shaw 1980; McPherson & Schmid 1991). The ancestral area of this subgenus is estimated to be Australia with subsequent dispersals to Papua New Guinea and New Caledonia during the Miocene (Fig. 9-2, clade F2). New Caledonia separated from Australia during the Mesozoic and discussions are ongoing whether it and the surrounding islands were completely submerged before the Eocene (Heads 2019). The flora is characterized by high levels of endemism (Pillon et al. 2017), which is also the case with *Dendrophyllanthus* (treated as *P.* subgenus *Gomphidium* in McPherson & Schmid 1991).

Sister to *Dendrophyllanthus* is clade F1, which corresponds to the genus *Cicca* of which the majority of species occur in Madagascar. Node F was reconstructed as Australia in the Bayarea analysis with low support (Table 9-3), and as Australia & Madagascar by the DEC model around the Mid-Oligocene. This relationship indicates an interesting connection and probable long distance dispersal between Australia and Madagascar (Fig. 9-2). However, it could also be due to incomplete sampling or possible extinction of taxa in areas between these distribution centers, but this cannot be inferred here. Within Clade F1, one group (*Cicca* subgenus *Cicca*) dispersed from Madagascar to Africa around and from there to South America during the Miocene.

Asian spread and diversification

More than 200 species of *Phyllanthus* s.l. occur in Asia and it has been suggested as the area where the genus originated (Govaerts et al. 2000). While this seems unlikely based on our results, Asia still harbours a large diversity of *Phyllanthus* species, which is a mix of several groups. The Asian genus *Nymphanthus* (previously *Phyllanthus* subgenus *Eriococcus*) with a crown age of 23.74 Ma (HPD 31.88–16.28) is reconstructed to have originated on continental Asia, with two independent movements into West Malesia in the Miocene (Fig. 9-2, node C4). Two species of *Nymphanthus* are known from Australia, but only *N. lamprophyllus* (Müll. Arg.) R.W.Bouman is included here and this species also crossed Wallace's line. It diverged from the Australian *Lysiandra* at the Eocene-Oligocene boundary. Another large Asian clade diverged from Node 8 with one group diverging into a clade comprising *Dendrophyllanthus* and the other giving rise to a large Malagasy and African clade.

The origin of the genera *Glochidion* and *Breynia* was inferred to be on the mainland of Asia (Fig. 9-2, node 9). The number of species of the genus *Glochidion* included here is limited and the inclusion of more species could lead to a different interpretation. As inferred here, *Glochidion* is a recently diverged lineage, which has speciated extensively, originating in the Late Miocene (Fig. 9-2). More than 300 species are currently recognized and their radiation has been attributed to a co-diversification with its pollinator (Kato et al. 2003; Kawakita & Kato, 2009). Our reconstruction of *Breynia* is comparable to the results by van Welzen et al. (2015), but their analysis discusses dispersal and vicariance at regional to country levels. The genus *Synostemon* consists of about 40 species and diverged from *Breynia* around 16 Ma (Fig. 9-2, node 11) as the lineage reached Australia and subsequently speciated there.

Diversification of tribe Phyllantheae

Phyllanthus s.l. is composed of several major clades showing distinctly different species numbers, some of which have been inferred to be linked to their specialized pollination system involving a mutualism with parasitic moths (Kato & Kato

2004a). This pollination system and variations of it have been found in several groups of tribe Phyllantheae, most notably in *Glochidion* (Kato et al. 2003), *Breynia* (Kwakita & Kato, 2004b), *Kirganelia* (Kawakita & Kato 2009; Kato & Kawakita 2017), *Dendrophyllanthus* (as *P*. subgenus *Gomphidium*; Kawakita & Kato 2004a) and with some indications for species from Madagascar (Kawakita & Kato 2009; Kato & Kawakita 2017) and the Neotropics (Kawakita et al. 2019). This mutualism has not always resulted in higher species numbers or speciation rates (Fig. 9-3). Speciation rates in *Kirganelia* were similar to *Nymphanthus* and *Cathetus*, for example (Table 9-4), which have been inferred to have different pollination systems (Luo et al. 2011b; Kato & Kawakita 2017). There are about 30 species in the palaeotropical *Kirganelia* (Bouman et al. 2018), which are often widespread and characterized by small pentamerous flowers and berries that are probably dispersed by birds. In contrast, there are more than 150 species in *Dendrophyllanthus* with most of this diversity found in Papua New Guinea and New Caledonia. *Glochidion* contains more than 300 species throughout Southeast Asia. While species in *Dendrophyllanthus* often have capsular fruits, fruits of *Glochidion* also dehisce to present brightly coloured sarcotestal seeds to attract birds. Bird dispersal seems to have resulted in species with wide distributions in *Kirganelia*, possibly constraining speciation rates, but similar patterns are not observed and should be further explored for *Glochidion* and *Dendrophyllanthus*. While the number of studies exploring the finesse and differences of this extraordinary pollination mutualism are steadily increasing, dispersal studies should be included to see how quickly genetic barriers can be raised between populations following isolation.

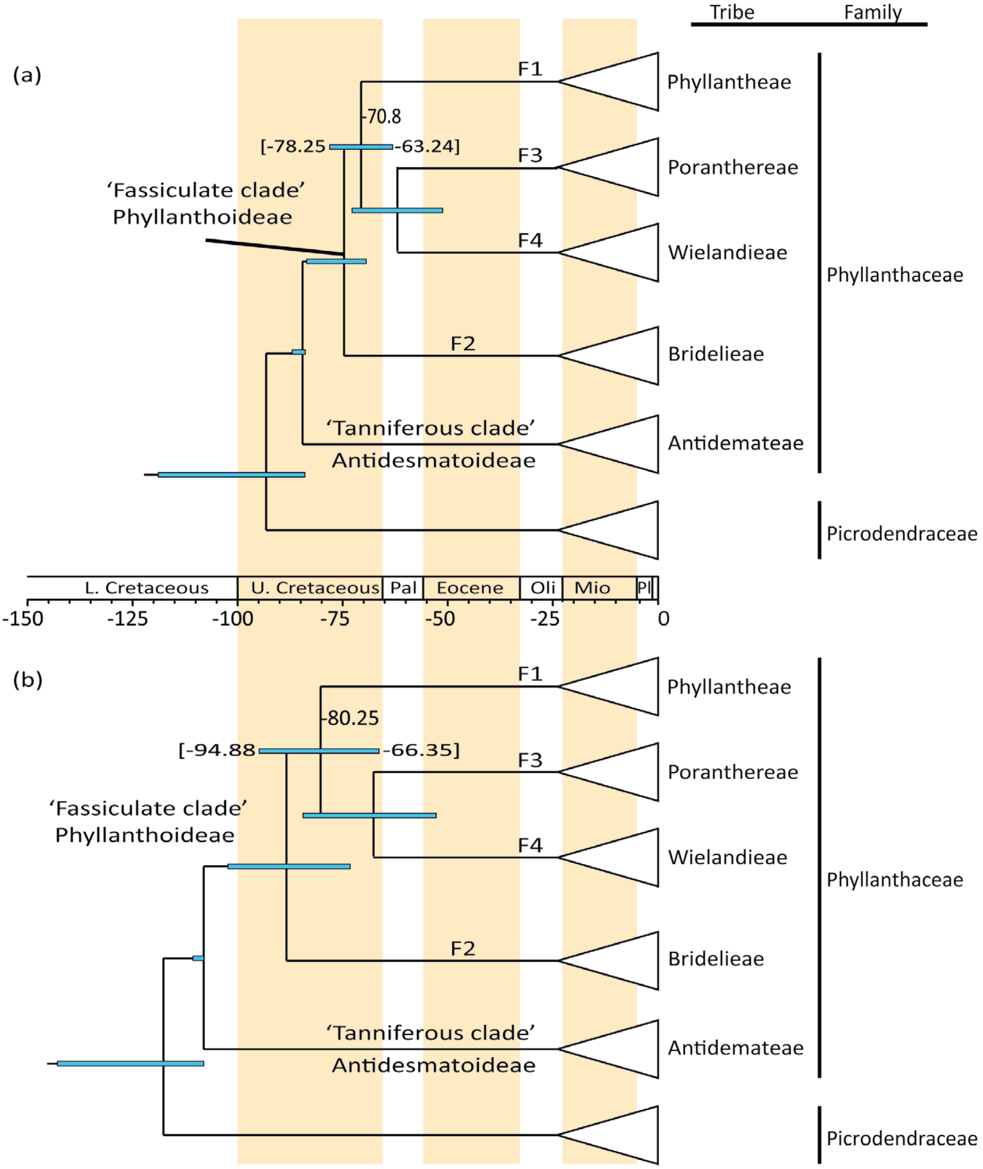
Conclusion

The evolutionary history of tribe Phyllantheae is explored here in more detail. The origin of *Phyllanthus* s.l. is dated to the Early Eocene, congruent with the PETM, while fossil findings in Europe hint at the possibility for a boreotropic origin and or migration pattern. Other theories, such as the Indian Raft hypothesis are unlikely to have played a role in the present distribution of the clade, but enhanced sampling of Indian taxa and taxa associated with *Nellica* (Clade A in Fig. 9-2) should be investigated in future studies to exclude this. Numerous dispersal events in the Cenozoic can be traced to the Miocene geothermal hypothesis or long-distance dispersal. Diversification rates were in general quite low, but a shift detected on node 8 (Fig. 9-2) could be linked to a starting pollination mutualism with moths (Kawakita & Kato 2009), although this was not the only factor as dispersal strategies seem to have constrained further speciation in other clades. Future studies should focus on detailing the various clades of tribe Phyllantheae, where the genera *Flueggea* and *Margaritaria* represent interesting pantropical taxa with bird-dispersed seeds.

Acknowledgments

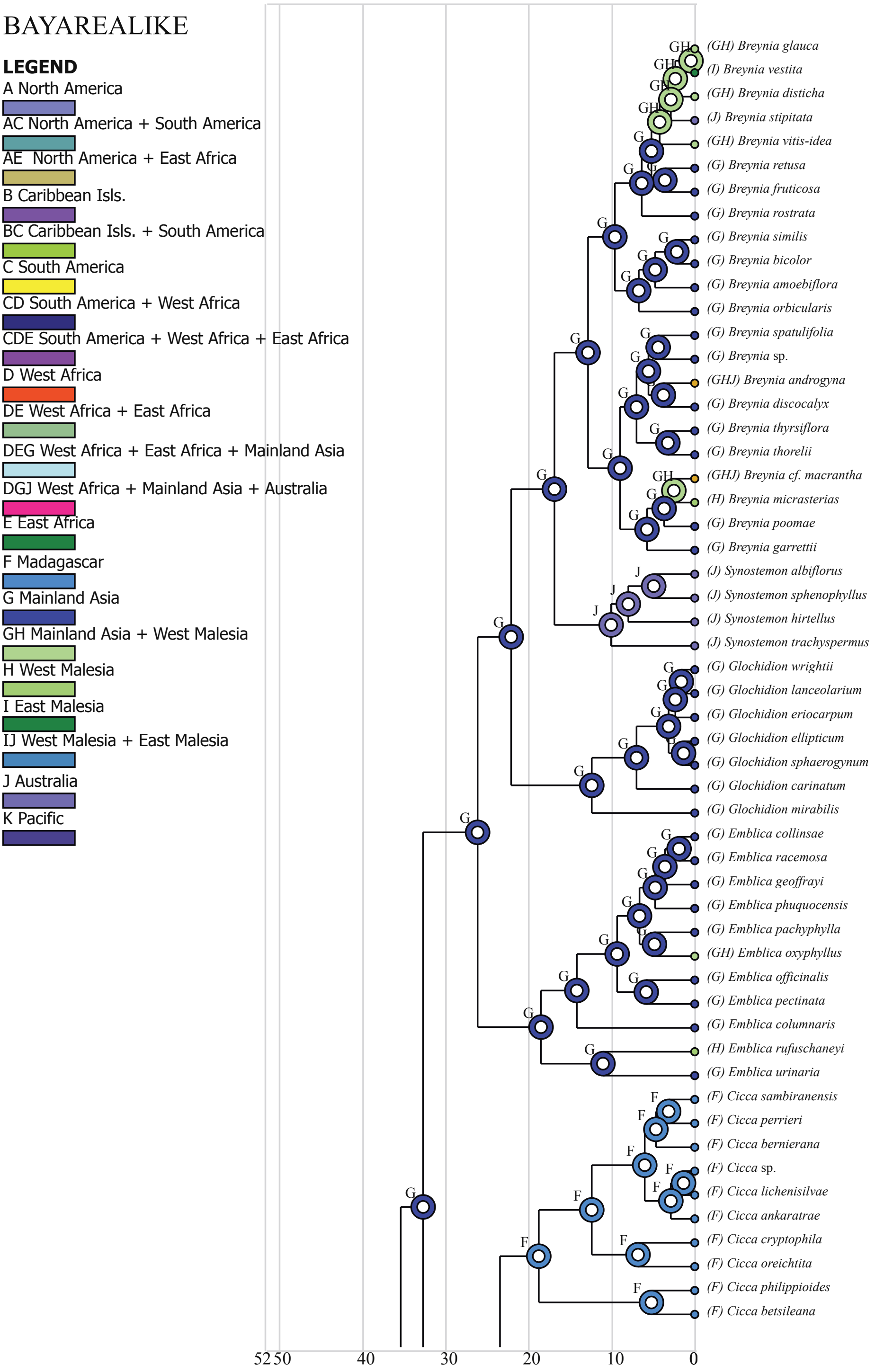
This work was done as part of the PhD research of the main author, funded by the Hortus botanicus Leiden (Leiden University) and hosted by Naturalis Biodiversity Center. The second author thanks the Leiden University Fund (LUF) for their support of the chair Botanical gardens and botany of Southeast 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.

Supplement



Supplementary figure S9-1. Summarized chronogram of Phyllanthaceae with tribes collapsed, relevant nodes are shown with 95% HPD; median age of divergence between tribe Phyllantheae and tribe Wielandieae and Poranthereae is given for the different reconstructions above HPD bar. (a) Chronogram of Phyllanthaceae with divergence age with Picrodendraceae constrained at 84 Ma. (b) Chronogram of Phyllanthaceae with divergence age with Picrodendraceae constrained at 108 Ma.

Supplementary figure S9-2. Ancestral area estimations of *Phyllanthus* and ingroup genera following the BAYAREA model. Distributions of taxa are shown at branch tips. Reconstructions on nodes with highest probability are shown. The figure is shown on pages 383 - 386. A full size pdf is available with the author.


BAYAREALIKE
LEGEND
A North America
AC North America + South America
AE North America + East Africa
B Caribbean Isls.
BC Caribbean Isls. + South America
C South America
CD South America + West Africa
CDE South America + West Africa + East Africa
D West Africa
DE West Africa + East Africa
DEG West Africa + East Africa + Mainland Asia
DGJ West Africa + Mainland Asia + Australia
E East Africa
F Madagascar
G Mainland Asia
GH Mainland Asia + West Malesia
H West Malesia
I East Malesia
IJ West Malesia + East Malesia
J Australia
K Pacific
(GH) Breynia glauca
(I) Breynia vestita
(GH) Breynia disticha
(J) Breynia stipitata
(GH) Breynia vitis-idea
(G) Breynia retusa
(G) Breynia fruticosa
(G) Breynia rostrata
(G) Breynia similis
(G) Breynia bicolor
(G) Breynia amoebiflora
(G) Breynia orbicularis
(G) Breynia spatulifolia
(G) Breynia sp.
(GHJ) Breynia androgyna
(G) Breynia discocalyx
(G) Breynia thyrsiflora
(G) Breynia thorelii
(GHJ) Breynia cf. macrantha
(H) Breynia micrasterias
(G) Breynia poomae
(G) Breynia garrettii
(J) Synostemon albiflorus
(J) Synostemon sphenophyllus
(J) Synostemon hirtellus
(J) Synostemon trachyspermus
(G) Glochidion wrightii
(G) Glochidion lanceolarium
(G) Glochidion eriocarpum
(G) Glochidion ellipticum
(G) Glochidion sphaerogynum
(G) Glochidion carinatum
(G) Glochidion mirabilis
(G) Emblica collinsae
(G) Emblica racemosa
(G) Emblica geoffrayi
(G) Emblica phuquocensis
(G) Emblica pachyphylla
(GH) Emblica oxyphyllus
(G) Emblica officinalis
(G) Emblica pectinata
(G) Emblica columnaris
(H) Emblica rufuschaneyi
(G) Emblica urinaria
(F) Cicca sambiranensis
(F) Cicca perrieri
(F) Cicca bernierana
(F) Cicca sp.
(F) Cicca lichenisilvae
(F) Cicca ankaratrae
(F) Cicca cryptophila
(F) Cicca oreichtita
(F) Cicca philippioides
(F) Cicca betsileana
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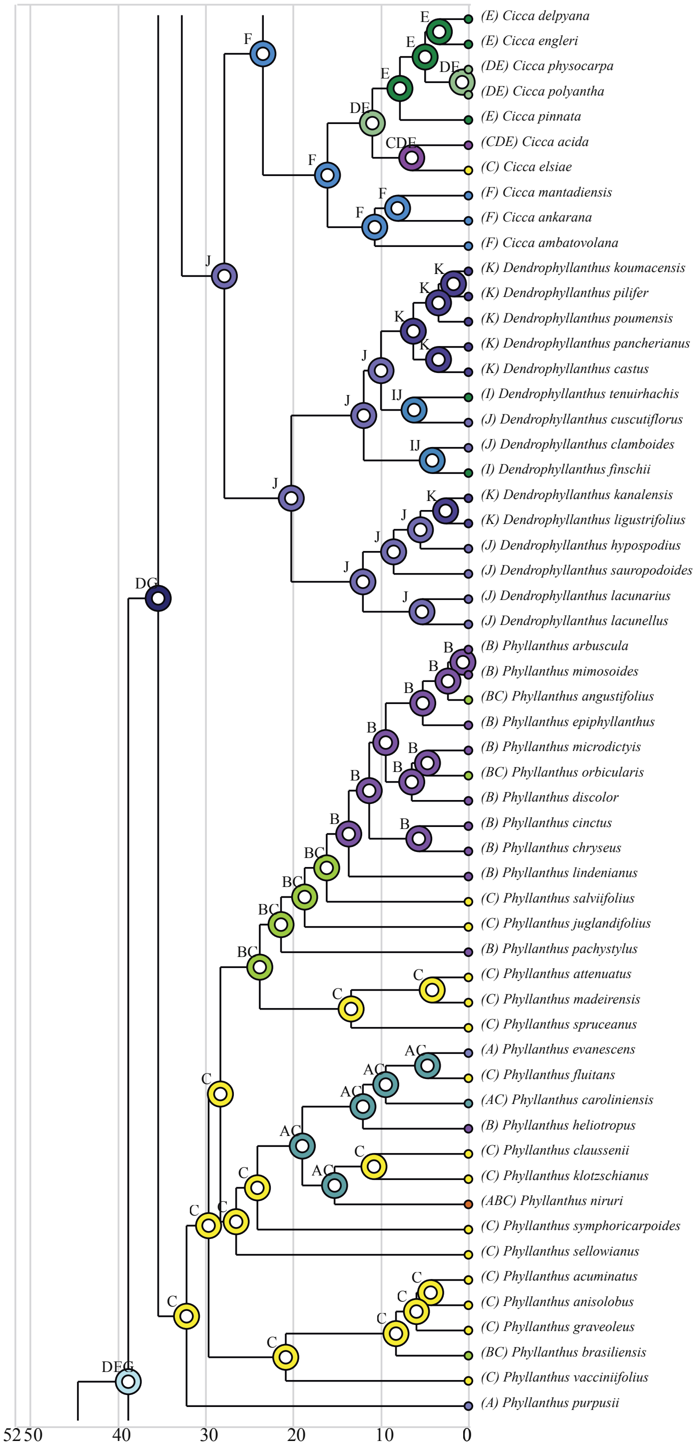
(E) Cicca delpyana
(E) Cicca engleri
(DE) Cicca physocarpa
(DE) Cicca polyantha
(E) Cicca pinnata
(CDE) Cicca acida
(C) Cicca elsiae
(F) Cicca mantadiensis
(F) Cicca ankarana
(F) Cicca ambatovolana
(K) Dendrophyllanthus koumacensis
(K) Dendrophyllanthus pilifer
(K) Dendrophyllanthus poumensis
(K) Dendrophyllanthus pancherianus
(K) Dendrophyllanthus castus
(I) Dendrophyllanthus tenuirhachis
(J) Dendrophyllanthus cuscutiflorus
(J) Dendrophyllanthus clamboides
(I) Dendrophyllanthus finschii
(K) Dendrophyllanthus kanalensis
(K) Dendrophyllanthus ligustrifolius
(J) Dendrophyllanthus hypospodius
(J) Dendrophyllanthus sauropodoides
(J) Dendrophyllanthus lacunarius
(J) Dendrophyllanthus lacunellus
(B) Phyllanthus arbuscula
(B) Phyllanthus mimosoides
(BC) Phyllanthus angustifolius
(B) Phyllanthus epiphyllanthus
(B) Phyllanthus microdictyis
(BC) Phyllanthus orbicularis
(B) Phyllanthus discolor
(B) Phyllanthus cinctus
(B) Phyllanthus chryseus
(B) Phyllanthus lindenianus
(C) Phyllanthus salviifolius
(C) Phyllanthus juglandifolius
(B) Phyllanthus pachystylus
(C) Phyllanthus attenuatus
(C) Phyllanthus madeirensis
(C) Phyllanthus spruceanus
(A) Phyllanthus evanescens
(C) Phyllanthus fluitans
(AC) Phyllanthus caroliniensis
(B) Phyllanthus heliotropus
(C) Phyllanthus claussenii
(C) Phyllanthus klotzschianus
(ABC) Phyllanthus niruri
(C) Phyllanthus symphoricarpoides
(C) Phyllanthus sellowianus
(C) Phyllanthus acuminatus
(C) Phyllanthus anisolobus
(C) Phyllanthus graveoleus
(BC) Phyllanthus brasiliensis
(C) Phyllanthus vacciniifolius
(A) Phyllanthus purpusii
F
J
DG
DEG
52
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20
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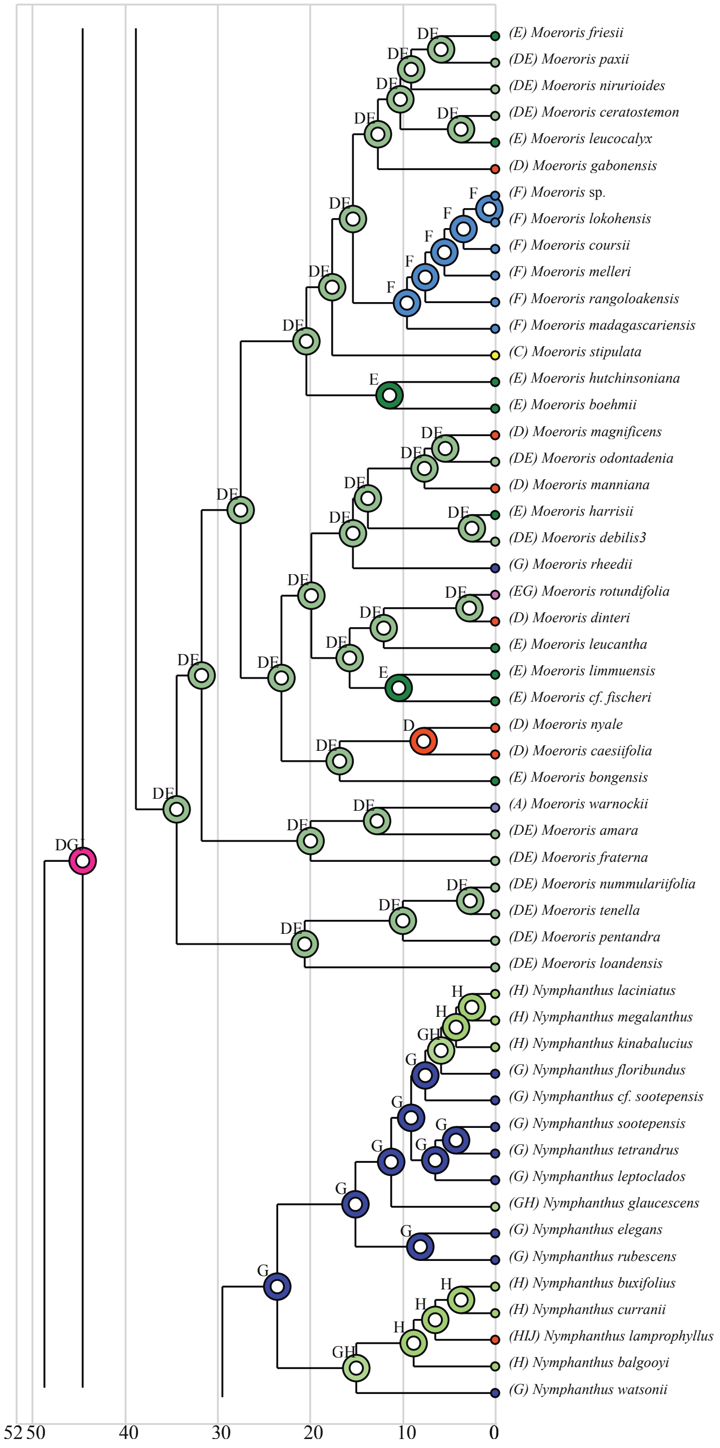
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(F) Moeroris madagascariensis
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(E) Moeroris boehmii
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(H) Nymphanthus kinabalucius
(G) Nymphanthus floribundus
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(H) Nymphanthus buxifolius
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(G) Nymphanthus watsonii
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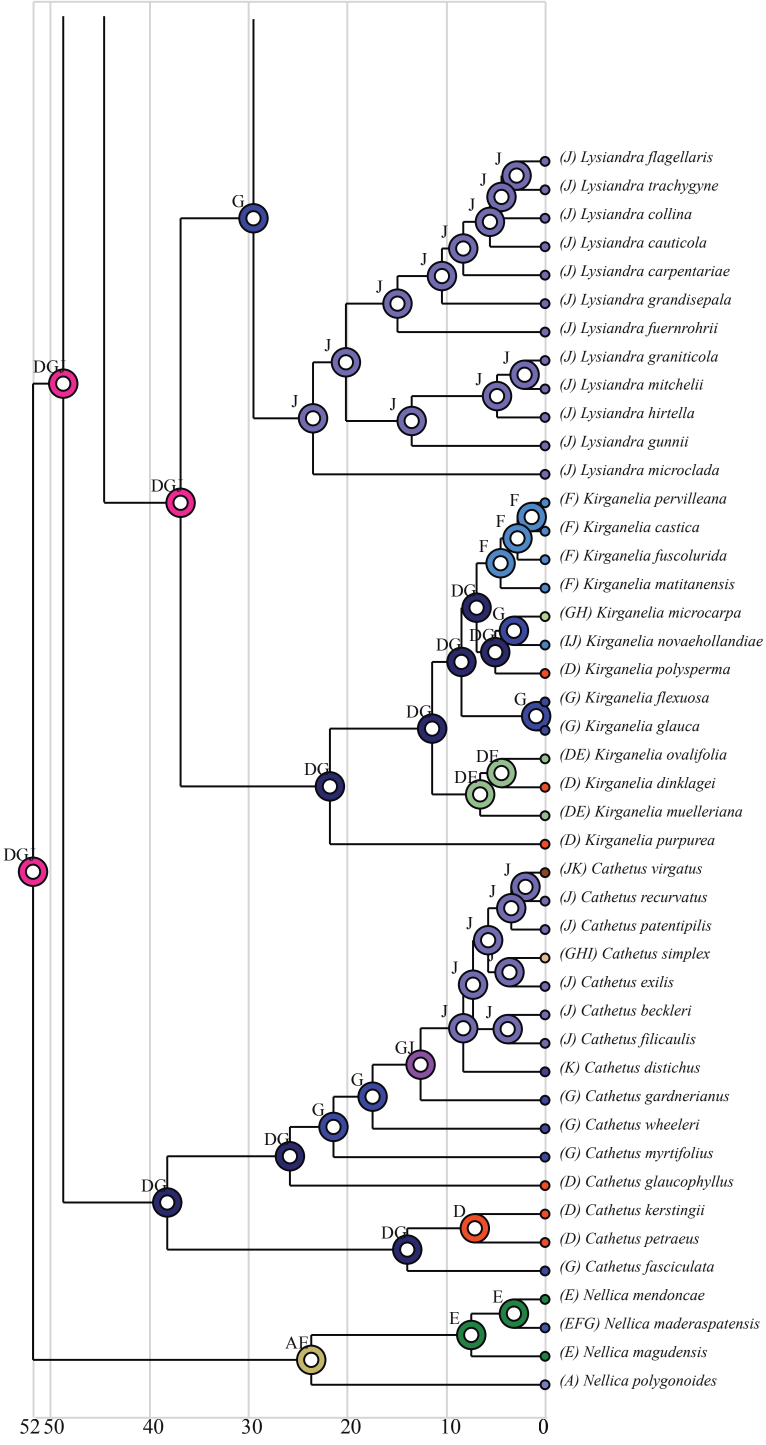
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(J) Lysiandra hirtella
(J) Lysiandra gunnii
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(J) Cathetus patentipilis
(GHI) Cathetus simplex
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(J) Cathetus beckleri
(J) Cathetus filicaulis
(K) Cathetus distichus
(G) Cathetus gardnerianus
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(G) Cathetus myrtifolius
(D) Cathetus glaucophyllus
(D) Cathetus kerstingii
(D) Cathetus petraeus
(G) Cathetus fasciculata
(E) Nellica mendoncae
(EFG) Nellica maderaspatensis
(E) Nellica magudensis
(A) Nellica polygonoides
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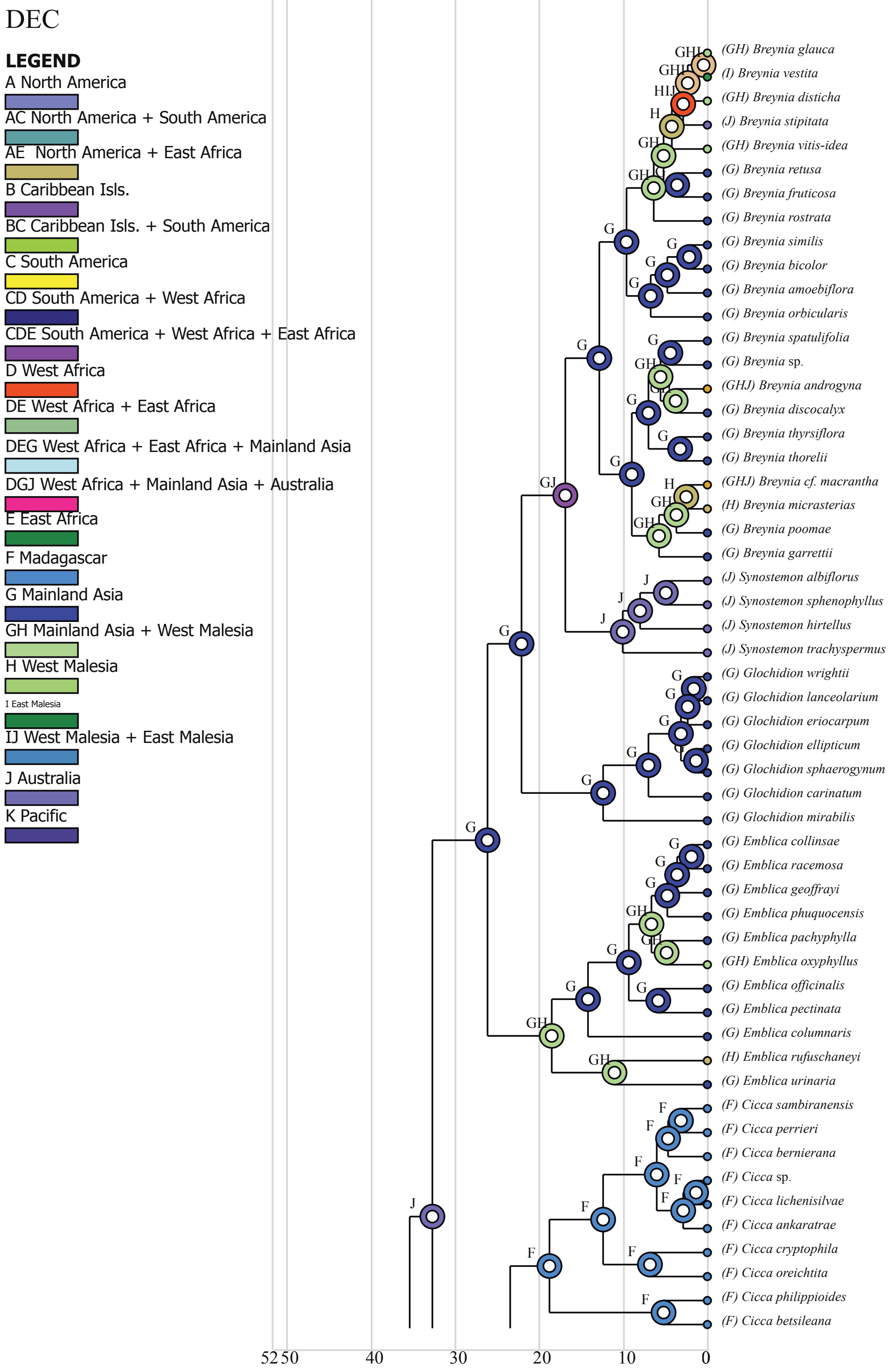
Supplementary figure S9-3. Ancestral area estimations of *Phyllanthus* and ingroup genera following the DEC model. Distributions of taxa are shown at branch tips. Reconstructions on nodes with highest probability are shown. The figure is shown on pages 388 - 391. A full size pdf is available with the author.


DEC
LEGEND
A North America
AC North America + South America
AE North America + East Africa
B Caribbean Isls.
BC Caribbean Isls. + South America
C South America
CD South America + West Africa
CDE South America + West Africa + East Africa
D West Africa
DE West Africa + East Africa
DEG West Africa + East Africa + Mainland Asia
DGJ West Africa + Mainland Asia + Australia
E East Africa
F Madagascar
G Mainland Asia
GH Mainland Asia + West Malesia
H West Malesia
I East Malesia
IJ West Malesia + East Malesia
J Australia
K Pacific
(GH) Breynia glauca
(I) Breynia vestita
(GH) Breynia disticha
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(G) Breynia amoebiflora
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(G) Breynia sp.
(GHJ) Breynia androgyna
(G) Breynia discocalyx
(G) Breynia thyrsiflora
(G) Breynia thorelii
(GHJ) Breynia cf. macrantha
(H) Breynia micrasterias
(G) Breynia poomae
(G) Breynia garrettii
(J) Synostemon albiflorus
(J) Synostemon sphenophyllus
(J) Synostemon hirtellus
(J) Synostemon trachyspermus
(G) Glochidion wrightii
(G) Glochidion lanceolarium
(G) Glochidion eriocarpum
(G) Glochidion ellipticum
(G) Glochidion sphaerogynum
(G) Glochidion carinatum
(G) Glochidion mirabilis
(G) Emblica collinsae
(G) Emblica racemosa
(G) Emblica geoffrayi
(G) Emblica phuquocensis
(G) Emblica pachyphylla
(GH) Emblica oxyphyllus
(G) Emblica officinalis
(G) Emblica pectinata
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(H) Emblica rufuschaneyi
(G) Emblica urinaria
(F) Cicca sambiranensis
(F) Cicca perrieri
(F) Cicca bernierana
(F) Cicca sp.
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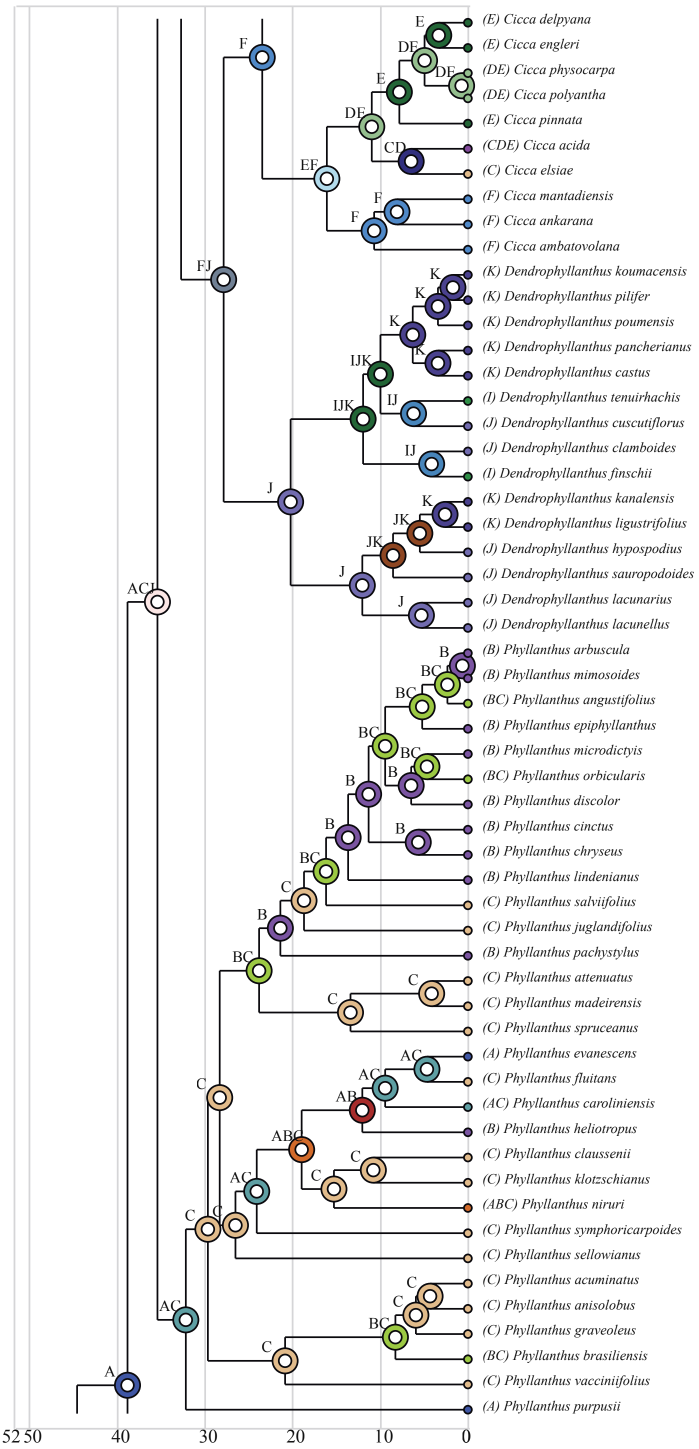
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(F) Cicca ankarana
(F) Cicca ambatovolana
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(A) Phyllanthus evanescens
(C) Phyllanthus fluitans
(AC) Phyllanthus caroliniensis
(B) Phyllanthus heliotropus
(C) Phyllanthus claussenii
(C) Phyllanthus klotzschianus
(ABC) Phyllanthus niruri
(C) Phyllanthus symphoricarpoides
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(C) Phyllanthus acuminatus
(C) Phyllanthus anisolobus
(C) Phyllanthus graveoleus
(BC) Phyllanthus brasiliensis
(C) Phyllanthus vacciniifolius
(A) Phyllanthus purpusii
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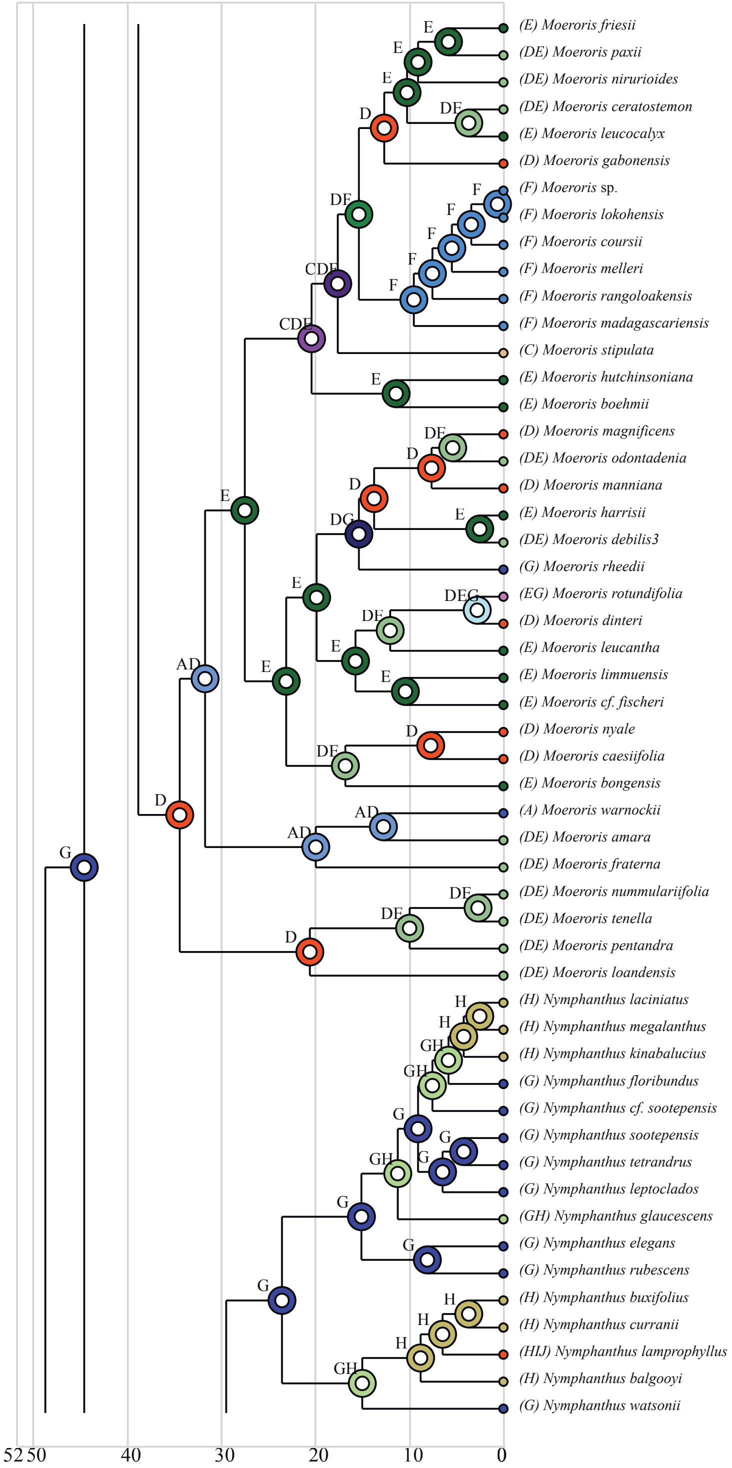
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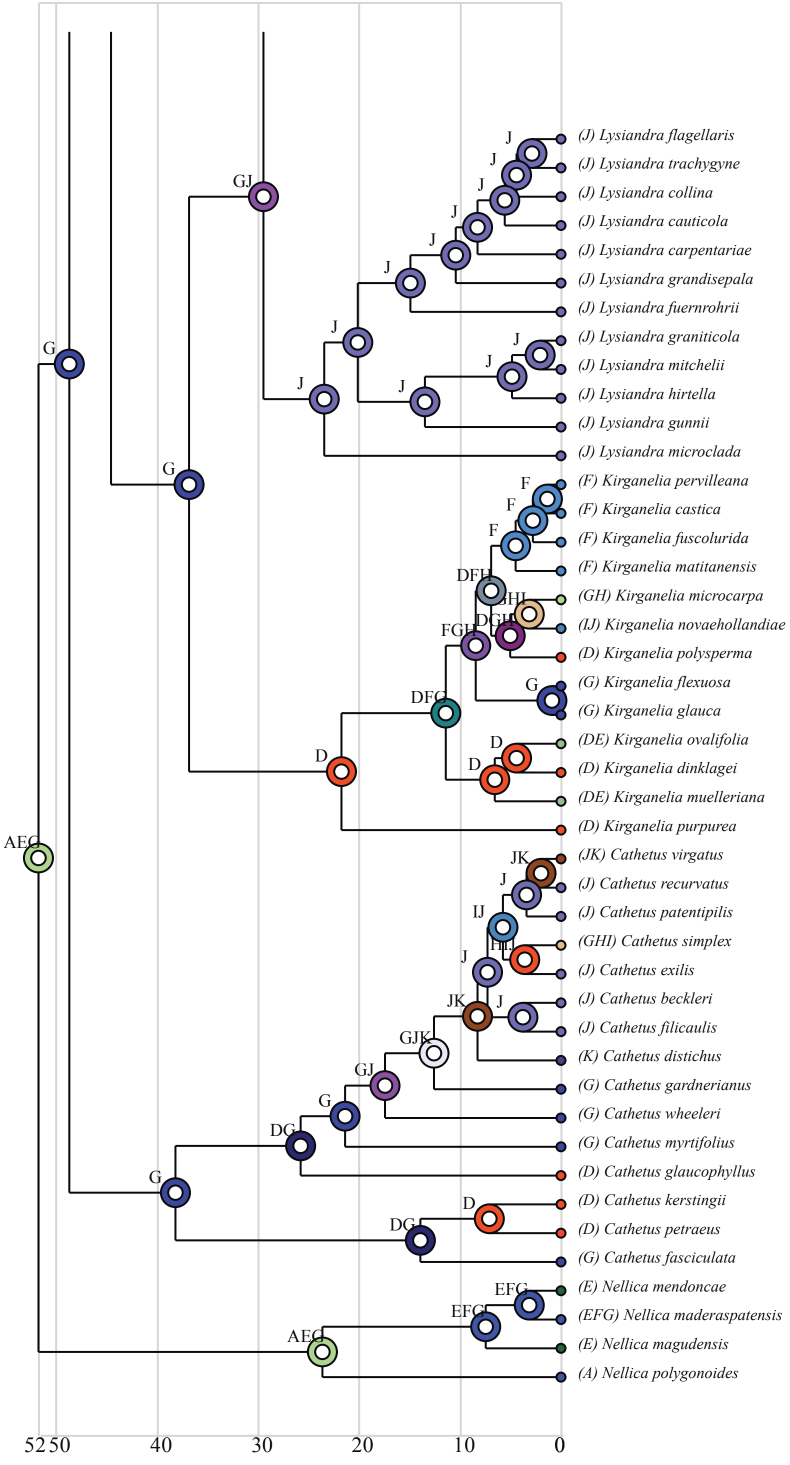
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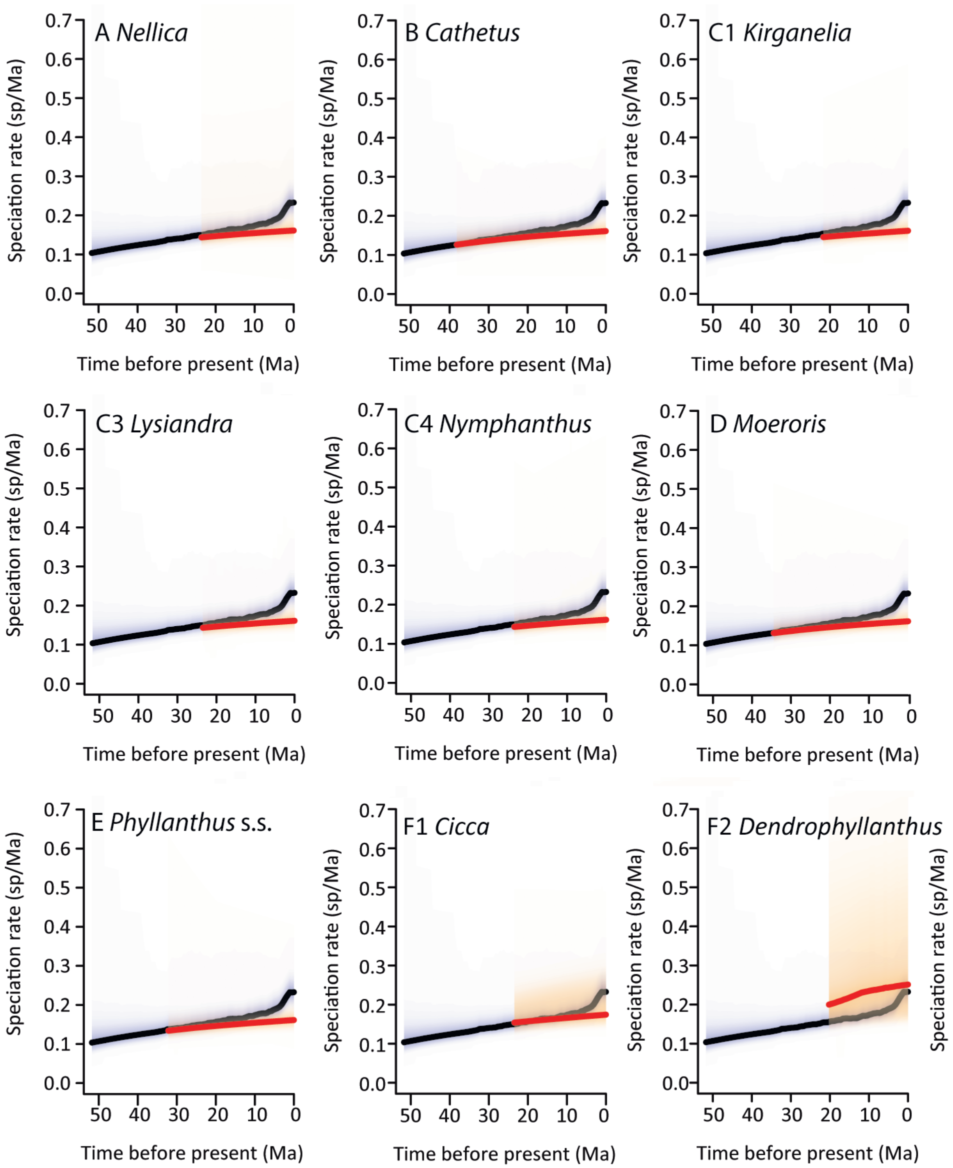
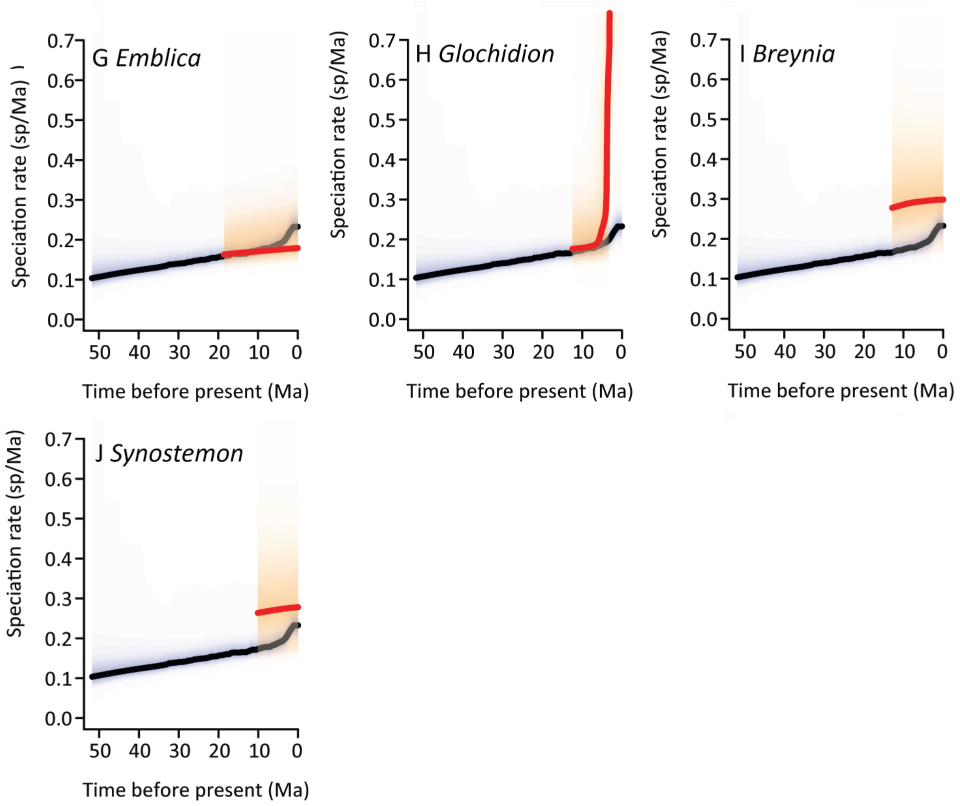


Supplementary figure S9-4. Additional plots of speciation rates through time of specific clades. Black line represents mean speciation rate through time of the whole phylogeny, red that of a selected clade.



Supplementary figure S9-4. Continued.

Supplementary table S9-1. Genbank accession numbers of DNA sequences and voucher information for taxa used in this study. Biogeographic regions follow figure 1: A, North America to Mexico; B, West Indies; C, South America and part of the Panama Isthmus; D, West Africa with eastern border following Namibia, Democratic Republic of Congo and Central African Republic; E, South and Eastern Africa; F, Madagascar and the Mascarene Islands; G, W. Asia stretching from India to Peninsular Malaysia; H, W. Malesia including Philippines; I, E. Malesia (mainly Papua New Guinea); J, Australia; K, Islands in the Pacific.

Matrix name	**Area code**	**Origin**	**ITS**	**PHYC**	***accD-psaI***	***matK***	***trnS-trnG***
Breynia amoebiflora	G	Chiang Mai, Thailand				EU643747	
Breynia amoebiflora	G	Thailand	GQ503379	GQ503437	GQ503498		GQ503562
Breynia androgyna	GHJ	Chachoengsao, Thailand	EU623563	GQ503439	GQ503500	EU643748	GQ503564
Breynia bicolor	G	Chiang Mai, Thailand	EU623567		GQ503503	EU643754	
Breynia cfmacrantha	GHJ	China (XTBG)	MN915813	MN904190	MN915297	MN916081	MN915580
Breynia discocalyx	G	Ranong, Thailand	GQ503387			EU643757	GQ503569
Breynia disticha	GH	Singapore botanical garden	MN915815	MN904192	MN915299	MN916083	MN915582
Breynia fruticosa	G	Hong Kong	MN915816	MN904193	MN915300	MN916084	MN915583
Breynia garrettii	G	Guinzhou, China	EU623570	GQ503444	GQ503507	EU643760	GQ503572
Breynia glauca	GH	Nong Khai, Thailand	EU623551	GQ503411		EU643737	GQ503532
Breynia micrasterias	H	Sarawak, Malaysia	EU623578	GQ503455		EU643768	GQ503582
Breynia orbicularis	G	Vientiane, Laos	EU623580	GQ503456	GQ503513	AY936645	GQ503584
Breynia poomae	G	Chiang Rai, Thailand	EU623582	GQ503457	GQ503515	EU643771	GQ503586
Breynia retusa	G	Sri Lanka				AY936565	
Breynia retusa	G	Vientiane, Laos	GQ503358	GQ503417	GQ503477		GQ503536
Breynia rostrata	G	China (XTBG)	MN915817	MN904194	MN915301	MN916086	MN915585

Breynia similis	G	Chiang Mai, Thailand	GQ503399	GQ503462	GQ503520	EU643778	GQ503592
Breynia sp.	G	Thailand	MN915843	MN904215	MN915327	MN916112	MN915600
Breynia spatulifolia	G	Honolulu, U.S.A.	EU623588		GQ503523	AY936647	GQ503596
Breynia stipitata	J	RBG Kew, Living collection from Queensland, Australia				AY552422	
Breynia stipitata	G	Australia	GQ503359	GQ503418	GQ503478		GQ503537
Breynia thorelii	G	Chiang Mai, Thailand	EU623590	GQ503468	GQ503526	EU643782	GQ503600
Breynia thyrsiflora	G	Kanchanaburi, Thailand	EU623591	GQ503469	GQ503527	EU643783	GQ503601
Breynia vestita	I	Papua, Indonesia	EU623553	GQ503419	GQ503480	EU643738	GQ503540
Breynia vitis-idea	GH	Singapore botanical garden	MN915822	MN904187	MN915306	MN916090	MN915587
Cathetus beckleri	J	Australia	MN915861	MN904231	MN915347	MN916127	MN915618
Cathetus distichus	K	Hawai'i	MN915912	MN904276	MN915404	MN916163	MN915665
Cathetus exilis	J	Australia	MN915922	MN904283		MN916362	MN915672
Cathetus fasciculata	G	Hong Kong	MN915895	MN904262	MN915384	MN916154	MN915648
Cathetus filicaulis	J	Australia	MN915923	MN904284	MN915415	MN916170	MN915673
Cathetus gardnerianus	G	Sri Lanka	AY936694	MN904314	MN915429	AY936598	MN915684
Cathetus glaucophyllus	DE	Guinea	MN915939	MN904318	MN915433	MN916340	MN915688
Cathetus kerstingii	D	Guinea	MN915950	MN905074	MN915447	MN916189	MN915701
Cathetus myrtifolius	G	Hong Kong University campus	MN915995	MN904370	MN915495	MN916214	MN915736
Cathetus patentipilis	J	Australia	MN916020	MN904392	MN915518	MN916234	MN915759
Cathetus petraeus	D	Liberia	MN916026	MN904397	MN915524	MN916239	MN915763
Cathetus recurvatus	J	Australia	MN916046	MN904414	MN915543	MN916258	MN915778

Cathetus simplex	G	Hong Kong	MN916074	MN904440	MN915572	MN916276	MN915805
Cathetus virgatus	J	Australia	AY936738	MN904442	MN915574	AY936639	MN915807
Cathetus wheeleri	G	Sri Lanka	AY936740	MN904445	MN915577	AY936641	MN915810
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Cicca ambatovolana	F	Madagascar	MN915848	MN904218	MN915332	MN916115	MN915605
Cicca ankarana	F	Madagascar	MN915851	MN904221	MN915335	MN916118	MN915608
Cicca ankaratrae	F	Madagascar	MN915852	MN904222	MN915336	MN916119	MN915609
Cicca bernierana	F	Madagascar	MN915862	MN904232	MN915348	MN916128	MN915619
Cicca betsileana	F	Madagascar	MN915863	MN904233	MN915349	MN916360	MN915620
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Cicca elsiae	C	Venezuela	MN915916	MN904278	MN915408	MN916337	MN915667
Cicca engleri	E	Tanzania		MN905066	MN915410	MN916168	MN915669
Cicca lichenisilvae	F	Madagascar		MN904343	MN915464	MN916199	
Cicca mantadiensis	F	Madagascar	MN915980	MN904354	MN915480	MN916319	
Cicca oreichtita	F	Madagascar	MN916013	MN904385		MN916226	
Cicca perrieri	F	Madagascar	MN916024	MN904395	MN915522	MN916238	MN915762
Cicca philippioides	F	Madagascar	MN916027	MN904398	MN915525	MN916240	MN915764
Cicca physocarpa	DE	Gabon	MN916030	MN904401	MN915528	MN916243	MN915766
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Cicca polyantha	DE	Cameroon	MN916033		MN915531	MN916246	MN915767
Cicca sambiranensis	F	Madagascar	MN916053	MN904421	MN915552	MN916315	MN915784
Cicca sp.	F	Madagascar	MN915845	MN904295	MN915329	MN916282	
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Dendrophyllanthus clamboides	J	Australia	MN915893	MN904260	MN915382	MN916152	MN915646
Dendrophyllanthus cuscutiflorus	IJ	Singapore botanical garden origin East Malesia	MN915901	MN904268	MN915392	MN916299	MN915654
Dendrophyllanthus finschii	I	Papua New Guinea	MN915924	MN904285	MN915416	MN916171	MN915674
Dendrophyllanthus hypospodius	J	Australia		GQ503435	GQ503495	EU643744	GQ503559
Dendrophyllanthus kanalensis	K	New Caledonia	AY936701			AY936604	
Dendrophyllanthus koumacensis	K	New Caledonia	MN915953	MN904331	MN915451	MN916191	
Dendrophyllanthus lacunarius	J	Australia	MN915955	MN904333	MN915453	MN916312	MN915706
Dendrophyllanthus lacunellus	J	Australia	MN915956	MN904334	MN915454	MN916313	MN915707
Dendrophyllanthus ligustrifolius	K	New Caledonia	MN915966	MN904309	MN915466	MN916311	MN915714
Dendrophyllanthus pancherianus	K	New Caledonia	AY936721	MN904391	MN915517	AY936623	MN915758
Dendrophyllanthus pilifer	K	New Caledonia	MN916031	MN904402	MN915529	MN916244	
Dendrophyllanthus poumensis	K	New Caledonia	MN916039	MN904408	MN915537	MN916251	MN915772
Dendrophyllanthus sauropodoides	J	Australia	EU623558	GQ503436	GQ503496	EU643745	GQ503560

Dendrophyllanthus tenuirhachis	I	Bogor botanical garden	MN916068	MN904435	MN915567	MN916271	MN915800
Emblcia oxyphylla	G	Thailand	MN916018	MN904388	MN915515	MN916232	MN915755
Emblcia pectinata	G	Singapore botanical garden origin Mainland Asia	MN916022		MN915520	MN916236	MN915761
Emblcia phuquocensis	G	Cambodia	MN916029	MN904400	MN915527	MN916242	
Emblcia racemosa	G	Sri Lanka	MN916035	MN904405	MN915533	MN916248	MN915769
Emblica collinsae	G	Thailand	MN915896	MN904263	MN915385	MN916155	MN915649
Emblica columnaris	G	Myanmar		MN904302	MN915387	MN916157	MN915651
Emblica geoffrayi	G	Thailand	MN915936	MN904315	MN915430	MN935816	MN915685
Emblica officinalis	G	Myanmar	MN915917	MN904279	MN915409	MN916167	MN915668
Emblica pachyphylla	G	Viet Nam	MN915853	MN904223	MN915337	MN916120	
Emblica rufuschaneyi	H	Borneo		MN904418	MN915547	MN916259	MN915781
Emblica urinaria	G	Hortus botanicus Leiden, origin Costa rica	MN916072	MN904438	MN915570	MN916274	MN915803
Flueggea virosa		China (XTBG)	MN915824	MN904197	MN915308	MN916091	
Glochidion carinatum	G	Cambodia		MN904243	MN915363	MN916138	
Glochidion ellipticum	G	China (XTBG)	MN915827	MN904200	MN915311	MN916094	MN915590
Glochidion eriocarpum	G	Hong Kong	MN915828	MN904201		MN916095	MN915592
Glochidion lanceolarium	G	China (XTBG)	MN915830	MN904203	MN915312	MN916097	MN915593
Glochidion mirabilis	G	Thailand	HM132100	HM132101	HM132099		HM132102
Glochidion sphaerogynum	G	Thailand	MN915831	MN904204	MN915313	MN916280	MN915594

Glochidion wrightii	G	Hong Kong	MN915832	MN904205	MN915314	MN916098	MN915595
Kirganelia castica	F	Madagascar	MN915878	MN904244	MN915366	MN916141	
Kirganelia dinklagei	E	Gabon	MN915908	MN904273	MN915399	MN916333	MN915660
Kirganelia flexuosa	GH	Myanmar	MN915929	MN904288	MN915421	MN916172	MN915679
Kirganelia fuscolurida	F	Madagascar	MN915934	MN904296	MN915426	MN916179	
Kirganelia glauca	G	Hong Kong	MN915940	MN904291	MN915434	MN916175	MN915689
Kirganelia matitanensis	F	Madagascar	MN915981	MN904355	MN915481	MN916205	
Kirganelia microcarpa	G	China (XTBG)	MN915985	MN904358	MN915483	MN916207	MN915729
Kirganelia muelleriana	DE	Zambia	MN915992	MN904368	MN915492	MN916212	MN915734
Kirganelia novae-hollandiae	J	Australia	MN916001	MN904376	MN915500	MN916219	MN915741
Kirganelia pervilleana	F	Madagascar	MN916025	MN904396	MN915523	MN916351	
Kirganelia polysperma	DE	Ethiopia	MN916036	MN904386	MN915534	MN916230	MN915771
Kirganelia purpurea	E	Namibia	MN916042	MN904411	MN915540	MN916254	MN915775
Leptopus chinensis		Cultivated Edinburgh Botanical garden	MN915833	MN904206	MN915315	MN916099	
Lysiandra carpentariae	J	Australia	MN915877	MN905063	MN915365	MN916140	MN915631
Lysiandra cauticola	J	Australia	MN915881	MN904247	MN915369	MN916303	MN915633
Lysiandra collina	J	Australia		MN904264	MN915386	MN916156	MN915650
Lysiandra fuernrohrii	J	Australia		MN904294		MN916178	
Lysiandra grandisepalus	J	Australia	MN915942	MN904319	MN915436	MN916289	MN915690
Lysiandra graniticola	J	Australia	MN915943	MN904320	MN915437	MN916185	MN915691
Lysiandra gunnii	J	Australia	MN915944	MN904322	MN915439	MN916290	MN915693
Lysiandra hirtella	J	Australia	MN915947	MN904326	MN915442	MN916187	MN915697

Lysiandra microclada	J	Australia	MN915988	MN904362	MN915487	MN916320	MN915730
lysiandra mitchelii	J	Australia	MN915990	MN904365	MN915490	MN916210	MN915733
Lysiandra trachygyne	J	Australia	MN916069	MN904436	MN915568	MN916294	MN915801
Margaritaria discoidea		Kenya		MN904207	MN915316	MN916101	
Margaritaria indica		Singapore botanical garden		MN904209	MN915318	MN916105	
Margaritaria nobilis		Puerto Rico		MN904210	MN915319	MN916106	MN915596
Margaritaria Uganda		Uganda	MN915835	MN904211	MN915320	MN916107	MN915597
Moeroris amara	DE	Thailand	EU623557	GQ503433	GQ503493	EU643742	GQ503557
Moeroris arenaria	A	USA (Texas)	AY936743	AY830380		AY830280	
Moeroris boehmii	E	Kenya	MN915865	MN904234	MN915351	MN916129	MN915622
Moeroris bongensis	E	Ethiopia	MN915868	MN904305	MN915355	MN916284	
Moeroris caesiifolius	D	Cameroon	MN915875	MN904242	MN915362	MN916137	MN915629
Moeroris ceratostemon	E	Tanzania	MN915882	MN904248	MN915370	MN916142	MN915634
Moeroris cf.fischeri	E	Ethiopia	MN915887	MN905067	MN915375	MN916343	MN915725
Moeroris coursii	F	Madagascar	MN915898	MN904266	MN915389	MN916329	
Moeroris debilis	DE	Philippines	MN915905	MN904271	MN915396	MN916332	MN915658
Moeroris dinteri	E	Namibia	MN915911	MN905069	MN915402	MN916336	MN915663
Moeroris flagellaris	J	Australia	MN915926	MN904287	MN915418	MN916307	MN915676
Moeroris fraternus	AE	Pakistan	MN915931		MN915423	MN916306	MN915681
Moeroris friesii	E	Zambia	MN915932	MN904293	MN915424	MN916177	MN915682
Moeroris gabonensis	D	Gabon	MN915935	MN904313	MN915428	MN916182	
Moeroris harrisii	E	Tanzania	MN915945	MN904323	MN915440	MN916341	MN915694
Moeroris hutchinsoniana	E	Zimbabwe	AY936697	MN904327	MN915443	AY936601	MN915698

Moeroris leucantha	E	Ethiopia	MN915963	MN904340	MN915461	MN916344	MN915713
Moeroris leucocalyx	E	Tanzania	MN915964	MN904342	MN915463	MN916198	
Moeroris limmuensis	E	Ethiopia	MN915967	MN904345	MN915467	MN916291	MN915715
Moeroris loandensis	E	Malawi	MN915968	MN904346	MN915469	MN916201	MN915717
Moeroris lokohensis	F	Madagascar	MN915971	MN904347		MN916316	
Moeroris madagascariensis	F	Madagascar	MN915973	MN904348	MN915473	MN916317	
Moeroris magnificens	D	Guinea	MN915975	MN904349	MN915475	MN916345	MN915722
Moeroris manniana	E	Cameroon	MN915977	MN904351	MN915477	MN916347	MN915724
Moeroris melleri	F	Madagascar	MN915983	MN904357	MN915482	MN916314	MN915728
Moeroris nirurioides	DE	Gabon	MN915999	MN904375	MN915498	MN916218	MN915740
Moeroris nummulariifolia	DEF	Tanzania	MN916005	MN904379	MN915504	MN916222	
Moeroris nyale	D	Cameroon	MN916008	MN904382	MN915507	MN916224	MN915746
Moeroris odontadenia	DE	Utrecht botanical garden	MN916010	MN904383	MN915509	MN916349	MN915748
Moeroris ovalifolia	DE	Ethiopia	MN916016	MN904301	MN915514	MN916229	MN915753
Moeroris paxii	E	Tanzania	MN916021	MN904393	MN915519	MN916235	MN915760
Moeroris pentandrus	E	Malawi	MN916023	MN904394	MN915521	MN916237	
Moeroris rangoloakensis	F	Madagascar	MN916045	MN904413	MN915542	MN916257	MN915777
Moeroris rheedii	G	Sri Lanka	AY936729	MN904415	MN915544	AY936630	MN915779
Moeroris rotundifolius	E	Kenya	MN916047	MN904416	MN915545	MN916352	MN915780
Moeroris sp.	F	Madagascar	MN915846		MN915330	MN916281	
Moeroris stipulata	C	Suriname	MN916062	MN904431	MN915562	MN916269	MN915794

Moeroris tenella	J	Australia	MN916065	MN904433	MN915564	MN916354	MN915797
Nellica maderaspatensis	F	Madagascar	AY936707			AY936609	
Nellica magudensis	DE	Sudan	MN915976	MN904350	MN915476	MN916318	MN915723
Nellica mendoncae	E	Ethiopia	MN915984				
Nellica polygonoides	A	USA (Texas)	MN916034	MN904404	MN915532	MN916247	MN915768
Notoleptopus decaisnei		Australia	AM745836			AM745833	
Notoleptopus decaisnei		Australia		GQ503431	GQ503491		GQ503555
Nymphanthus aff. curranii	H	Philippines	MN915900	MN904267	MN915391	MN916158	MN915604
Nymphanthus balgooyi	H	Philippines	MN915860	MN904230	MN915346	MN916325	MN915617
Nymphanthus buxifolius	H	Singapore botanical garden	MN915873	MN904240	MN915360	MN916326	MN915627
Nymphanthus elegans	G	Viet Nam	MN915915	MN904277	MN915407	MN916166	
Nymphanthus floribundus	G	Sri Lanka	AY936682	MN904259	MN915381	AY936587	
Nymphanthus glaucescens	G	Thailand	MN916041	MN904410	MN915539	MN916253	MN915774
Nymphanthus kinabalucius	H	Borneo	MN915952	MN904330	MN915449	MN916190	MN915703
Nymphanthus laciniatus	H	Philippines	MN915954	MN904332	MN915452	MN916192	MN915705
Nymphanthus lamprophyllus	J	Australia	MN915959	MN904337	MN915457	MN916195	MN915710
Nymphanthus leptoclados	G	China (XTBG)	MN915961	MN904339	MN915459	MN916196	MN915712

Nymphanthus megalanthus	H	Philippines	MN915982	MN904356		MN916206	MN915727
Nymphanthus rubescens	G	Viet Nam	MN916048	MN904417	MN915546	MN916322	
Nymphanthus sootepensis	G	Myanmar	MN916059	MN904426	MN915558	MN916297	MN915790
Nymphanthus tetrandrus	G	Myanmar	MN916058	MN904425	MN915557	MN916296	MN915789
Nymphanthus watsonii	G	Peninsular Malaysia	MN916076	MN904444	MN915576	MN916278	MN915809
Phyllanthus acuminatus	C	Guatemala	MN915838	MN904213	MN915322	MN916110	MN915599
Phyllanthus angustifolius	B	Bayreuth botanical garden living collection origin Carribean	MN915849	MN904219	MN915333	MN916116	MN915606
Phyllanthus anisolobus	C	Costa Rica	MN915850	MN904220	MN915334	MN916117	MN915607
Phyllanthus arbuscula	B	Meisse living collection origin Carribean	MN915855	MN904226	MN915339	MN916123	MN915610
Phyllanthus attenuatus	C	Venezuela	MN915856	MN904304	MN915341	MN916125	MN915612
Phyllanthus brasiliensis	C	Peru, Loreto, Pongo de Cainarachi	MN915871	MN904236	MN915358	MN916135	MN915626
Phyllanthus caroliniensis	ABC	Suriname	MN915876		MN915364	MN916139	MN915630
Phyllanthus cf.sootepensis	G	China (XTBG)	MN915890	MN904428	MN915378	MN916267	MN915643
Phyllanthus chryseus	B	Cuba	AY936681	MN904257	MN915379	AY936586	MN915644
Phyllanthus cinctus	B	Cuba	MN915892	MN904258	MN915380	MN916151	MN915645

Phyllanthus claussenii	C	Minas Gerais	MN915894	MN904261	MN915383	MN916153	MN915647
Phyllanthus discolor	B	Cuba	AY936688	MN904275	MN915403	AY936593	MN915664
Phyllanthus epiphyllanthus	B	Meisse living collection	MN915919	MN904280	MN915412	MN916169	MN915671
Phyllanthus evanescens	AC	Nicaragua	MN915921	MN904282	MN915414	MN916339	
Phyllanthus fluitans	C	Cultivated Botanical garden Bonn	MN915930	MN904292	MN915422	MN916176	MN915680
Phyllanthus graveolens	C	Ecuador	AY936696	MN904321	MN915438	AY936600	MN915692
Phyllanthus heliotropus	B	Cuba	MN915946	MN904325	MN915441	MN916186	MN915696
Phyllanthus juglandifolius	C	Cultivated, Hortus botanicus Amsterdam origin South America	MN915949	MN904328	MN915445	MN916188	MN915699
Phyllanthus klotzschianus	C	Brazil	AY936702			AY936605	
Phyllanthus lindenianus	B	Dominican Republic	LS975755			LS975815	
Phyllanthus lindenianus	B	Dominican Rep.			MN915468		MN915716
Phyllanthus madeirensis	C	Brazil	MN915974	MN905078	MN915474	MN916293	MN915721
Phyllanthus microdictyis	B	Cuba	AY936709	MN904363	MN915488	AY936612	MN915731
Phyllanthus mimosoides	B	Meisse living collection origin Carribean	MN915989	MN904364	MN915489	MN916209	MN915732
Phyllanthus niruri	C	Bolivia	MN916000	MN904373	MN915499	MN916217	
Phyllanthus orbicularis	B	Cuba	MN916012	MN904298	MN915511	MN916225	MN915750

Phyllanthus pachystylus	B	Cuba	AY936720	MN904390	MN915516	AY936622	MN915757
Phyllanthus purpusii	A	Mexico, now cultivated Berkeley	MN916043	MN904412	MN915541	MN916255	MN915776
Phyllanthus salviifolius	C	Ecuador	MN916052	MN904420	MN915551	MN916262	MN915783
Phyllanthus sellowianus	C	Kew living collection	MN916056	MN904424	MN915555	MN916265	MN915787
Phyllanthus spruceanus	C	Guyana	MN916061	MN904429	MN915560	MN916353	MN915792
Phyllanthus symphoricarpoides	C	Colombia	MN916064	MN904307	MN915563	MN916321	MN915796
Phyllanthus vacciniifolius	C	Venezuela	MN916073	MN904439	MN915571	MN916275	MN915804
Synostemon albiflorus	J	Australia	MN916077	MN904446	MN915578	MN916279	MN915811
Synostemon hirtellus	J	Queensland, Australia	EU623573	GQ503447	GQ503508	EU643763	GQ503574
Synostemon sphenophyllus	J	Queensland, Australia	GQ503402	GQ503465		EU643780	GQ503597
Synostemon trachyspermus	J	Australia	GQ503407	GQ503470	GQ503528	EU643784	GQ503602

Supplementary table S9-2. Matrices with dispersal rate scaling used in reconstruction under the dispersal-extinction-cladogenesis model (DEC). Biogeographic regions follow figure 1: A, North America to Mexico; B, West Indies; C, South America and part of the Panama Isthmus; D, West Africa with eastern border following Namibia, Democratic Republic of Congo and Central African Republic; E, South and Eastern Africa; F, Madagascar and the Mascarene Islands; G, W. Asia stretching from India to Peninsular Malaysia; H, W. Malesia including Philippines; I, E. Malesia (mainly Papua New Guinea); J, Australia; K, Islands in the Pacific. Green marks an increase in dispersal rates, while yellow marks a decrease compared to older periods.

32-60 Ma	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
A	1	1	0,5	1	0,01	0,01	1	0,01	0,01	0,01	0,01
B	1	1	0,5	0,5	0,01	0,01	0,01	0,01	0,01	0,01	0,01
C	0,5	0,5	1	0,75	0,25	0,01	0,01	0,01	0,01	0,25	0,01
D	1	0,5	0,75	1	1	0,5	1	0,5	0,01	0,01	0,01
E	0,01	0,01	0,25	1	1	1	0,5	0,5	0,01	0,01	0,01
F	0,01	0,01	0,01	0,5	1	1	0,5	0,5	0,5	0,5	0,01
G	1	0,01	0,01	1	0,5	0,5	1	1	0,01	0,01	0,01
H	0,01	0,01	0,01	0,5	0,5	0,5	1	1	0,5	0,5	0,01
I	0,01	0,01	0,01	0,01	0,01	0,5	0,01	0,5	1	0,75	0,75
J	0,01	0,01	0,25	0,01	0,01	0,5	0,01	0,5	0,75	1	0,75
K	0,01	0,01	0,01	0,01	0,01	0,01	0,01	0,01	0,75	0,75	1

5-32 MA	A	B	C	D	E	F	G	H	I	J	K
A	1	1	1	0,01	0,01	0,01	0,01	0,01	0,01	0,01	0,01
B	1	1	1	0,5	0,01	0,01	0,01	0,01	0,01	0,01	0,01
C	1	1	1	0,5	0,01	0,01	0,01	0,01	0,01	0,01	0,01
D	0,01	0,5	0,5	1	1	0,5	0,75	0,5	0,01	0,01	0,01
E	0,01	0,01	0,01	1	1	1	0,75	0,5	0,01	0,01	0,01
F	0,01	0,01	0,01	0,5	1	1	0,5	0,5	0,5	0,5	0,01
G	0,01	0,01	0,01	0,75	0,75	0,5	1	1	0,5	0,5	0,01
H	0,01	0,01	0,01	0,5	0,5	0,5	1	1	0,5	0,01	0,01
I	0,01	0,01	0,01	0,01	0,01	0,5	0,5	0,5	1	0,75	0,75
J	0,01	0,01	0,01	0,01	0,01	0,5	0,5	0,01	0,75	1	0,75
K	0,01	0,01	0,01	0,01	0,01	0,01	0,01	0,01	0,75	0,75	1

0-5 MA	A	B	C	D	E	F	G	H	I	J	K
A	1	1	1	0,01	0,01	0,01	0,01	0,01	0,01	0,01	0,01
B	1	1	1	0,25	0,01	0,01	0,01	0,01	0,01	0,01	0,01
C	1	1	1	0,25	0,01	0,01	0,01	0,01	0,01	0,01	0,01
D	0,01	0,25	0,25	1	1	0,5	0,5	0,5	0,01	0,01	0,01
E	0,01	0,01	0,01	1	1	1	0,5	0,5	0,01	0,01	0,01
F	0,01	0,01	0,01	0,5	1	1	0,5	0,5	0,5	0,5	0,01
G	0,01	0,01	0,01	0,5	0,5	0,5	1	1	0,75	0,5	0,01
H	0,01	0,01	0,01	0,5	0,5	0,5	1	1	1	0,75	0,25
I	0,01	0,01	0,01	0,01	0,01	0,5	0,75	1	1	1	0,75
J	0,01	0,01	0,01	0,01	0,01	0,5	0,5	0,75	1	1	0,75
K	0,01	0,01	0,01	0,01	0,01	0,01	0,01	0,25	0,75	0,75	1

CHAPTER 10

Conclusions

Chapter 10. Conclusions

General discussion

Phyllanthus L. sensu lato (s.l.) is known as a diverse clade with often difficult to distinguish species due to the small flowers and the often high resemblance in leaf shapes and sizes. In this thesis I explored the evolution of this group while also proposing an alternative classification as a solution to the apparent paraphyly (not all descendents of an ancestral species included). Initial work by Linneaus (1753, 1778) and De Jussieu (1803) already indicated a diversity of characters that were used to place the species in different genera. After Müller (11863, 1865, 1866) defined *Phyllanthus* as one genus with over 40 different sections, the biggest update to this system was implemented by Webster (1956, 1957, 1958 and thereafter). Webster focused on the West Indian and American species of *Phyllanthus*, but treatments for other floristic regions were scattered and a global inventory of the number of accepted species was overdue. The systematic history was summarised in chapter 3 in the form of a list, which included all accepted species and their infrageneric placement to that point. While Webster published many treatments for the Neotropical flora, the Palaeotropics remained understudied. The first of these groups to be treated was *Phyllanthus* subgenus *Macraea* (Wight) Jean F.Brunel (Chapter 4). Follow-up revisions that focus on other groups are now also being progressed (Wibowo et al. unpublished; Hinloopen et al. unpublished).

By increasing our understanding of the relationship between groups in tribe Phyllantheae while revising various groups to look for synapomorphies, this thesis presents another option to the apparent paraphyly of *Phyllanthus*, which has been under discussion already for several years. Also an investigation in the metabolites of several species was included as this field keeps growing and the interest in *Phyllanthus*, already substantial in traditional medicines, is increasing.

How large is the diversity of Phyllanthus and tribe Phyllantheae and how is it structured?

Our initial review of the long taxonomic history of *Phyllanthus* resulted in a list containing 880 species, which could be classified into 18 subgenera and 70 accepted sections (chapter 3). A few overlooked issues were found that needed to be addressed. *Phyllanthus* subsections *Callidisci* Jean F.Brunel and *Odontadenii* Jean F.Brunel & Jacq.Roux had been placed in a large concept of *Phyllanthus* subgenus *Phyllanthus* by Brunel (1987). However, the phylogenetic study of Kathriarachchi et al. (2006) had already shown that this subgenus was polyphyletic and a new subgenus was subsequently created with the goal of housing the African and Malagasy species in the revision work by Ralimanana & Hoffmann (2011, 2014). Their work did not take into account the subsections defined by Brunel (1987). In chapter 3 we transferred these subsections, but also specifically listed all species that we hypothesized to be included in subgenus *Afroswartziani* Ralim. & Petra Hoffm.

Other changes, in *Phyllanthus* subgenus *Gomphidium* (Baill.) G.L.Webster, were also included based on recommendations in Webster's manuscripts that were never completed or published.

Additional changes to the number of species in *Phyllanthus* came with the revision of one of the understudied subgenera (chapter 4) and the study of some poorly known species from Sulawesi (chapter 5). The revision of *Phyllanthus* subgenus *Macraea* included 24 species with indications that there might be a few more in India. It is a Palaeotropical group with the majority of its diversity in Asia and previously species of this group were only treated separately for local floras. This group of species is characterized by non-phyllanthoid branching, 3-merous flowers with three free stamens and clypeate pollen. The constituent species were expanded to include species from the Philippines and the Pacific, indicating that *P.* subgenus *Macraea* is distributed from Africa all the way to Hawai'i.

Koorders (1898) published two species of *Phyllanthus* for the island of Sulawesi, but only included a concise description, which precluded assignment to any subgenus. After studying the specimens collected by him, we lectotypified these species and also concluded that they should be placed in *Phyllanthus* subgenus *Eriococcus* (chapter 5). They are most likely related to similar looking species from the Philippines of which one appeared to be synonymous. These species likely belong to a lineage that might have originated on the mainland and dispersed through the Philippines to Sulawesi and ultimately reached the Lesser Sunda islands.

The infrageneric framework outlined in chapters 2–5 provided the best hypothesis to test for monophyletic groups as potential candidates to be integrated in a re-classification of *Phyllanthus* s.l. A phylogenetic study of five molecular markers found several problems with the previous system, most commonly due to monospecific taxa or small sections, which were found to be embedded in other groups (chapter 7). Some subgenera like *Phyllanthus* subgenus *Gomphidium* and *Kirganelia* were found to be polyphyletic and the paraphyly of *Phyllanthus* was again confirmed. *Phyllanthus* s.l. appeared to consist of eight separate clades with *Glochidion* closely related to a paraphyletic *Phyllanthus* subgenus *Phyllanthodendron*. A new classification has to correct for these findings, but could focus on these clades as potentially separate genera.

Medicinal properties of Phyllanthus

Species of *Phyllanthus* s.l. are used in various traditional medicines. Plant metabolomics using Proton nuclear magnetic resonance (HNMR) combined with anti-bacterial and anti-fungal testing provided a strong method to study these effects and potentially find bioactive compounds, which could be targets for future studies. Unfortunately our results were minimal as only a few extracts of species were found to possess antibacterial effects. Most likely due to concentration issues we could not determine which compounds were responsible for these effects. A survey across the literature showed that more and more compounds are discovered in tribe Phyllantheae every year and potentially a study of the related species suggested by our phylogenetic work, can identify new candidates for future work.

Monophyletic or monophyletic, large versus small genera

The paraphyletic nature of *Phyllanthus* s.l. was one of the main focuses of this thesis. After indications from Wurdack et al. (2004) and confirmation by Kathriarachchi et al. (2006), a new classification of tribe Phyllantheae sought to combine *Phyllanthus* with *Breynia*, *Sauropus* and *Glochidion* (Hoffmann et al. 2006). *Phyllanthus* would be monophyletic when combining all embedded groups, but also by creating a new classification by dividing the genus into smaller genera based on clades and recognisability. However, creating one giant genus would temporarily solve the problem and identifications issues would just be pushed to subgeneric levels. A broader treatment of *Phyllanthus* would still result in a few hundred species needing to be transferred, while *Phyllanthus* becomes a giant genus with no apparent synapomorphies. Christenhusz (2020) advocated for a conservative approach in naming with increasingly larger genera on the basis that it would be more stable as it would be easier to maintain monophyly. As long-standing genera have large bodies of literature attached to them, dividing genera into new groups would ignore the relations between clades and their evolutionary history. Then what to do with paraphyletic groups? Christenhusz (2020) indicated that these should not be accepted, but instead create larger groups and look for similarities between the clades (giving an example of birds and reptiles). Applying this to *Phyllanthus*, would result in a group with no distinct synapomorphy and the characters that differ between clades are equal or larger than the difference between *Phyllanthus* s.l. and *Flueggea* Willd., *Margaritaria* L.f. and the rest of tribe Phyllantheae. The alternative approach presented here, might not work in other genera, but actively avoiding one side of the argument is not good science.

In chapter 9 we present our classification of tribe Phyllantheae with 18 genera based on the results from our phylogenetic and morphological work. A new phylogeny is presented by combining the contemporous studies of Chapter 7 and Falcón et al. (2020). *Phyllanthus* s.s. is restricted to mostly the Neotropics while the genera *Cathetus* Lour., *Cicca* L., *Dendrophyllanthus* F.Muell., *Emblica* Gaertner, *Kirganelia* A.Juss, *Moeroris* Raf., *Nellica* Raf. and *Nymphanthus* Lour. are reinstated and *Lysiandra* (F.Muell.) R.W.Bouman, I.Telford & J.J.Bruhl is raised to the level of genus. Each genus is (re-)described while taking into account all previously defined subgroupings of which not all are retained. Especially a number of monospecific sections are subsumed in larger groups. While we present a more conservative approach in the number of subgenera and (sub)sections of the various genera, we feel that this classification

Morphological evolution

The large morphological diversity found in *Phyllanthus* s.l. could already be seen in the large number of subgenera and sections. The flowers show large differences between taxa while there are also some interesting oddities. While studying the phylogeny of tribe Phyllantheae, it became apparent that some morphological features thought to be indicative of common ancestry, were actually the result of convergent evolution (chapter 7).

The specific type of branching found in the majority of species of tribe Phyllantheae, the so called phyllanthoid branching, sets it apart of other members of the Phyllanthaceae. It is likely that this branching system is involved with energy management and maximizing photosynthetic potential. How this system exactly works and whether nutrients flows are reversed is not known. The ability to shed whole branchlets and have leaves on the main stem reduced to scales provides the plants with a great system for energy management and to prevent light competition between its own branchlets while keeping a slim habit.

Staminate flowers usually show little difference between species in a particular clade, but they are invaluable for distinguishing genera. Early diverged clades in *Phyllanthus* s.l. have trimerous flowers with two perianth whorls and this trait seems to be conserved in parts throughout the phylogeny. Pentamerous flowers originated independently at least six times. In contrast pistillate flowers show more differences in the shape of the style and stigmas related to different pollination systems and these can be used to differentiate species.

Capsules are common fruits in the Phyllanthaceae family, but several instances are found in tribe Phyllantheae, where berries have evolved.

Dispersal history

The reconstruction of *Phyllanthus* showed that it likely originated somewhere in the Early Eocene and possibly in the boreotropics. Early dispersals to North America, Africa and Asia have lead to the present day distribution of the reinstated *Nellica*, a clade sister to the rest of *Phyllanthus* s.l. The diversification of *Flueggea* and *Margaritaria* is of a more recent date, which suggests that their pantropical distribution is also an effect of more recent long-distance dispersals than a boreotropical origin. Initial results indicated that boreotropical dispersal might have influenced the distribution of several clades, with *Nellica* present in North America, Africa and Asia, while some clades only show major distribution centers in Asia and Africa (*Cathetus* and *Moeroris*). Subsequent dispersal out of Africa to the Neotropics are inferred to have occurred during the Oligocene, which lead to *Phyllanthus* sensu stricto (s.s.; here the only clade retained as *Phyllanthus*, chapter 9). Within *Phyllanthus* s.s. several independent diserpsals northwards are found to Mexico, but also to the West Indies. From Africa, one clade also dispersed to Australia, which lead to *Cicca* and the very diverse *Dendrophyllanthus*. *Cicca* has a wide distribution with a few species in Asia to more diverse clades in Madagascar, Africa and again some species in the Neotropics, which seems to be the result of more recent dispersals. In mainland Asia, several groups diverged to form *Emblica*, *Glochidion*, *Breynia* (more explored in van Welzen et al. 2015) and with one dispersal event, which lead to *Synostemon* in mainly Australia.

Diversification of tribe Phyllantheae

Species diversity within *Phyllanthus* s.l. shows an uneven pattern, with some highly speciose clades seeming to be very young, while others that diverged earlier do not include as many species. A diversification analysis on the dated tree of chapter 8 showed two possible shifts in speciation. One was for the clade comprising the reinstated genera *Cicca* and *Dendrophyllanthus*, while the other occurred for the genus *Glochidion*. A high rate of speciation of tribe Phyllantheae had previously been related to a pollination mutualism with parasitic moths, but this pattern was not observed in all clades where this system has been inferred. Other factors such as dispersal strategy are proposed to have affected potential speciation rates, but a larger ecological study is necessary to understand this. As the pollination system is also found to vary between genera and also species, subtle nuances could also still have an effect. Highest speciation rates and the strongest shift was still found for *Glochidion* subgenus *Glochidion* and not as much in the former *Phyllanthodendron* attributed species. Species placed here in *G.* subgenus *Pseudoactephila* and *G.* subg. *Phyllanthodendron* were hypothesized to be pollinated perhaps by flies and some characters like the inflated fruits have previously been attributed as a defense against herbivory and seed predation (Kato & Kawakita 2017). The pollination mutualism with moths is hypothesized to have evolved from an original parasitic system (Kato & Kawakita 2017) and perhaps parasitism is present in more clades in the tribe, with some species evolving defences against this.

Future perspectives

This thesis investigated the global evolutionary patterns of *Phyllanthus* and how to translate these in a monophyletic classification at generic level. Studying other factors such as flower development and differences in ecology, could provide more insight in the evolution of the diverse tribe Phyllantheae. Especially ecological information on many species is lacking and as in many plant families, the life histories of the plants have barely been studied.

The pollination mutualism with parasitic moths has, since its first publication (Kato 2003), garnered much attention as an ideal study system for co-evolution and co-diversification of two groups. While the diversification rates for tribe Phyllantheae were studied here in relation to this mutualism, the amount of data on other ecological factors and variations in this system is very limited. Other ecological factors such as dispersal mechanics are also a field that presents interesting opportunities within tribe Phyllantheae. The phylogeny showed several shifts in fruit type, which probably indicate differences in dispersal vectors, but which vectors or how this is associated with speciation has not been studied. An interesting system could be in the genus *Cicca* where the fruits are capsules in the Malagasy clades, while in *C.* subgenus *Cicca* different types are found from small berries to apple-like fruits and inflated capsules that are a contender for the biggest fruits in the tribe.

As the speed and data originating from molecular tools is rapidly increasing, future studies might implement a much broader sampling of the genome of the various genera in tribe Phyllantheae. Initial studies have already sequenced the plastid genome of species of *Breynia* (Cai et al. 2019; Zhou et al. 2020), *Glochidion* (Cheon et al. 2019) and *Flueggea* (Wang et al. 2020) and as more information becomes available, it will be possible to study other aspects then phylogenetics such as genome duplication patterns or the evolution of gene function and composition. Indications of whole genome duplications in Phyllanthaceae have been found by Cai et al. (2019), but they only included two species of this family. Chromosome counts from Miller & Webster (1966) found that the base number in Phyllanthaceae (then Euphorbiaceae subfamily Phyllanthoideae) was $x = 13$ (also in Webster & Ellis 1962). The same base number has been found in species of *Flueggea*, *Margaritaria*, *Kirganelia*, *Nellica*, *Cathetus* (Webster & Ellis 1962; Hans 1973), while higher chromosome numbers are found in *Moeroris*, *Phyllanthus* s.s., *Breynia* and *Synostemon* (Webster & Ellis 1962; Miller & Webster 1966). This indicates at least one possible duplication or hybridisation event within tribe Phyllantheae with possibly more since some clades have species that are tetraploids (Hans 1973).

New taxonomic studies will continue on tribe Phyllantheae, however to prevent overlooked species, revision work should focus on separate taxa instead of local floras. Some taxa are in dire need of an updated treatment, like the reinstated genus *Emblica*, where its constituent species have always been scattered over several subgeneric groups. By understanding more of the phylogenetic context of each genus, it will be easier to make comparisons between groups of species to find more diagnostic characters between them. Following our new classification of tribe Phyllantheae, several genera are already geographically separated and once the genus is known, species identification becomes more narrow in this framework. Hopefully this will aid future taxonomists with their understanding of these awesome plants.

Final remarks

My journey with *Phyllanthus* has been long and interesting. Not all experiments succeeded and naturally not all species could be exhaustively treated. Still, I hope that the work presented in this thesis has demonstrated how wonderful the plants that made up *Phyllanthus* s.l. are. The species in the tribe Phyllantheae display an enormous variation in habit, flowers and fruit morphology, which is only indicative of a long and intricate evolutionary history and likely partly due to the moth pollination. I have attempted to redefine *Phyllanthus* s.l. and create a classification that shows this history, with reinstated genera that show where clades diverged, but which sometimes also showed convergent evolution. A new view on *Phyllanthus* and its related genera creates the way to actively compare clades and study how these evolved to lead to the diversity we see today.

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SUMMARY

In the past 50 years, plant systematics has undergone a revolution with the advent and rapid accessibility of molecular techniques, which greatly influenced how we study and classify taxa. While many organism groups and theories have been proven accurate, some appeared to be more complex than previously thought. The plant genus *Phyllanthus* (Phyllanthaceae tribe Phyllantheae) is a good example of a group of species with varying views on its taxonomy and it has always been treated as closely related to the genera *Glochidion*, *Breynia* (including *Sauropus*) and *Synostemon*. Previous studies found the latter genera to have developed within *Phyllanthus* and a proposal was made to merge all, thereby creating one giant genus with over 1200 species with an enormous variation in morphological features. To study the evolutionary history and possibilities in classification, we explored this genus in greater detail. A number of species of *Phyllanthus* are also used in traditional medicine and two well-known examples (*P. emblica* and *P. acidus*) are species grown for their their edible fruits that contain high numbers of vitamin C.

The genus *Phyllanthus* was first described by Linnaeus in 1753 and with subsequent publications over the past 250 years, this group has grown to include over 800 species. Some have been treated as separate genera by some authors, but in the 19th century clusters of similar species were united in one *Phyllanthus* and grouped in a classification below the genus level consisting of over 40 sections. From the 1950s onwards, the relation between these sections was organized in several subgenera. This classification was based on anatomy, which was expanded with the incorporation of various morphological features including habit, branching system and pollen morphology. However, taxon recognition often focused on specific regions instead of complete (sub) groups and in chapter 3 we compiled a checklist that incorporated all the subgroups that have been defined and placed almost all species in this framework. Almost all 800 species were in the framework, based on morphological features and past classifications, and it resulted in the recognition of 18 subgenera, 70 sections and 14 subsections. The various subgenera presented strong candidates for a new classification on genus level of *Phyllanthus* and the related genera. We followed up the checklist with the publication of a new species (chapter 2), a study on *P.* subgenus *Macraea* (chapter 4) which included species never placed in that group before and a study of the species described by Koorders for the island of Sulawesi (chapter 5).

The results from previous phylogenetic studies had included around 10% of the species of *Phyllanthus*. In our phylogenetic study based on five markers (chapter 6), we included species from all subgenera and 53 of the 70 sections, while discussing patterns of morphological evolution and several instances of convergent evolution. Characters such as the specialized branching system present in the majority of species, has been lost in several clades independently. Other features such as the loss of the nectar disk, or the simplified style and stigma morphology that is associated with a specific pollination system involving mutualistic moths is also indicated to have evolved several times. By comparing the phylogeny with the framework outlined in the checklist of chapter 3, we found multiple instances of paraphyletic subgroups often related to small (usually monospecific) taxa nested in other groups. However, the backbone phylogeny showed good support between major clades that are often morphologically distinct.

In addition to their diversity and evolution, *Phyllanthus* is also an interesting group with regards to the medicinal usage of several species. Species of *Phyllanthus* are used in various ways and extractions are also sold as tablets with vitamin supplements, to help kidney and liver function or to combat inflammation. A few species are grown in botanical gardens throughout Europe, which provided a great opportunity to study their antimicrobial and antifungal effects. In chapter 6 we sampled several species from the living collections of the Hortus botanicus Leiden and we used Proton Nuclear Magnetic Resonance (^{1}H NMR) to study their metabolite profiles. This was correlated with the results from a screening for bioactivity against *Escherichia coli* and *Staphylococcus aureus* and followed by a targeted approach using High Performance Thin Layer Chromatography (HPTLC). Indications were found for significant activity against gram-negative bacteria for *P. arbuscula, P. muellerianus, P. tenellus and P. urinaria*, but we were unable to identify the compounds that underly this. Future studies would need a larger sample set, but our results indicate that their focus could be especially on the phenolics produced by these species.

Following the results from our phylogenetic work, it was necessary to create a new classification for *Phyllanthus* and its related genera. While previous studies had proposed to merge everything, we decided to divide *Phyllanthus* into smaller segregates (Chapter 8). We reinstated the genera *Cathetus*, *Cicca*, *Dendrophyllanthus*, *Emblica*, *Kirganelia*, *Moeroris*, *Nellica* and *Nymphanthus* while *Lysiandra* was raised to the generic level. This retained the genera *Glochidion*, *Breynia* and *Synostemon* while creating a classification based on recognisable monophyletic groups. More than 600 species were transferred to another genus in this new classification. Several paraphyletic sections and subgenera are expanded to include the species nested within them. Both solutions to the paraphyly of *Phyllanthus* are valid, union of all or separation, but by dividing *Phyllanthus* into smaller groups as proposed here, the evolutionary history of the group is reflected in a much better way.

Using the phylogeny from chapter 5 we had previously looked at various morphological evolutionary patterns, but barely touched on the subject of how the whole tribe became so diverse and how it dispersed through time. While a broad treatment of *Phyllanthus*, considered it to be a pantropical genus, the reinstated segregate genera are often restricted to one or two continents. In chapter 9 we explain how the current distribution came to be and whether there have been shifts in its diversification. Traditionally the pantropical distribution of the clade has been attributed to a Gondwanan origin, but we found that tribe Phyllantheae probably originated during the Late Palaeocene close to the Palaeocene-Eocente Thermal Maximum (PETM). The genera *Nellica* and *Cathetus* indicate early dispersals between Africa and Asia, with the former genus also being present in North America. This distribution is consistent with a possible boreotropical origin followed by subsequent extinction in Europe. Fossil pollen findings in Europe also indicate that *Flueggea* or a related genus was present there at the time. Within clades/genera we found that their distribution is often the result of a limited number of dispersal events. While studying diversification rate shifts in the tribe, we found that the pollination mutualism present in several clades is not always consistent with an increase in diversification. In some clades, this did not lead to a higher rate of diversification and this is possibly caused but not fully explained by a difference in dispersal vectors/mechanisms.

The evolution of tribe Phyllantheae is explored here in relation to its systematics and dispersal history, but as outlined in chapter 10, many questions remain to be answered. Future studies can explore the evolution of specific clades and how the species diverged and adapted to different conditions. Especially the pollination mutualism with moths present in several clades provides a great opportunity to study how both pollinator and plant are locked in an evolutionary struggle and how they adapt to each other. In this thesis I have expanded upon our knowledge of the phylogeny of *Phyllanthus* and its related genera while trying to provide a system for all species that were attributed to it. While this classification may change again in the future, the tribe remains an interesting study group.

SAMENVATTING

De afgelopen 50 jaar was er een revolutie in de plantensystematiek met de komst en snelle en relatief goedkope toegankelijkheid van moleculaire technieken. Deze hebben een enorme invloed gehad op hoe taxa bestudeerd en geclassificeerd worden . Hoewel veel groeperingen van organismen en theorieën werden bewezen, is ook gebleken dat sommige complexer zijn dan eerder werd gedacht. Het plantengeslacht *Phyllanthus* (Phyllanthaceae-tribus (= stam) Phyllantheae) is een goed voorbeeld van een groep soorten waarbij vorige auteurs verschillende opvattingen hadden. Deze groep is altijd beschouwd als nauw verwant aan de geslachten *Glochidion*, *Breynia* (inclusief *Sauropus*) en *Synostemon*. Eerdere studies vonden dat de laatst genoemden ontstaan zijn binnen *Phyllanthus* en dat resulteerde in een voorstel om alles samen te voegen. Dit zou uitmonden in één gigantisch geslacht met meer dan 1200 soorten met een enorme variatie in morfologische kenmerken. Om de evolutionaire geschiedenis en mogelijkheden in classificatie te bestuderen, hebben we dit geslacht in detail onderzocht. Verscheidene soorten van *Phyllanthus* worden ook gebruikt in de traditionele geneeskunde en twee bekende voorbeelden zijn soorten die worden gekweekt voor hun eetbare vruchten die een hoog gehalte aan vitamine C bevatten.

Het geslacht *Phyllanthus* werd voor het eerst beschreven door Linnaeus in 1753 en door de daaropvolgende publicaties in de afgelopen 250 jaar is de groep gegroeid en bevat het meer dan 800 soorten. Sommige zijn door sommige auteurs als afzonderlijke geslachten behandeld, maar in de 19e eeuw werden clusters van vergelijkbare soorten gegroepeerd in een classificatie van meer dan 40 secties onder het geslachtsniveau. Vanaf de jaren vijftig van de 20ste eeuw werd de relatie tussen deze secties georganiseerd in verschillende ondergeslachten. Dit was een op anatomie gebaseerde classificatie die werd uitgebreid met de opname van verschillende morfologische kenmerken, waaronder groeivorm, vertakkingssysteem en pollenmorfologie. Floristische werken zijn meestal gericht op specifieke regio's in plaats van op (sub)groepen zodat een overzicht van alle soorten per groep ontbrak, daarom hebben we in hoofdstuk 3 een checklist samengesteld waarin alle gedefinieerde subgroepen zijn opgenomen met bijna alle soorten er in geplaatst. De verschillende ondergeslachten waren sterke kandidaten voor een nieuwe indeling van het geslacht *Phyllanthus* en de gerelateerde groepen in meerdere geslachten. We volgden de checklist op met de publicatie van een nieuwe soort (hoofdstuk 2), een studie over het ondergeslacht *Macraea* (hoofdstuk 4) met soorten die nog nooit eerder in die groep waren geplaatst en een studie van de soorten beschreven door Koorders voor het eiland Sulawesi (hoofdstuk 5). Bijna alle soorten waren in dit systeem geplaatst, gebaseerd op morfologische kenmerken en classificaties uit het verleden en het resulteerde in een indeling met 18 ondergeslachten, 70 secties en 14 subsecties.

De resultaten van eerdere fylogenetische studies waren gebaseerd op ongeveer 10% van het aantal soorten binnen *Phyllanthus* waarbij niet alle ondergeslachten waren bemonsterd. In onze fylogenetische studie, gebaseerd op vijf markers (hoofdstuk 6), hebben we soorten uit alle subgenera en 53/70 secties opgenomen terwijl we patronen van morfologische evolutie en verschillende gevallen van convergente evolutie bespraken. Een kenmerk zoals het gespecialiseerde vertakkingssysteem dat in de meeste soorten aanwezig is, is in verschillende takken van de stamboom onafhankelijk van elkaar verloren gegaan. Er is ook een specialistisch bestuivingssysteem met mutalistische motten en in dit systeem hebben de bloemen vaak geen nectarschijf meer en zijn de stijl en stempel simpeler of geslotener dan bij andere systemen. Deze kenmerken lijken een aantal keren onafhankelijk te zijn geëvolueerd. Door de fylogenie te vergelijken met de groepenindeling van de soortenlijst van hoofdstuk 3, vonden we meerdere gevallen van parafyletische subgroepen (niet alle soorten die afstammen van een voorouder verenigd). Vaak werd dit veroorzaakt doordat kleinere taxa met meestal maar één soort genesteld waren in grotere groepen. De stamboom toonde een sterke ondersteuning voor de grotere groepen die vaak ook morfologisch verschillend zijn.

Naast hun diversiteit en evolutie is *Phyllanthus* ook een interessante groep met betrekking tot het medicinaal gebruik van verschillende soorten. Verscheiden soorten worden gebruikt tegen verschillende kwaaltjes en sommige worden ook verkocht als vitaminesupplementen of om de nier- en leverfunctie te ondersteunen. Een paar soorten komen voor in botanische tuinen in Europa, wat een geweldige kans bood om hun antimicrobiële en antischimmeleffecten te bestuderen. In hoofdstuk 6 hebben we verschillende soorten uit de levende collecties van de Hortus botanicus Leiden bemonsterd en hebben we Proton Nuclear Magnetic Resonance (1H NMR) gebruikt om hun metabolietprofielen in kaart te brengen. Dit werd vergeleken met de resultaten van een screening op bioactiviteit tegen *Escherichia coli* en *Staphylococcus aureus* en vervolgens gebruikten we High Performance Thin Layer Chromatography (HPTLC). Voor *P. arbuscula*, *P. muellerianus*, *P. tenellus* en *P. urinaria* werden aanwijzingen gevonden voor significante activiteit tegen gramnegatieve bacteriën, maar de onderliggende stoffen konden we helaas niet identificeren. Toekomstige studies zouden een grotere steekproefset nodig hebben, maar onze resultaten geven aan dat hun focus zou kunnen liggen op de fenolen die door deze soorten worden geproduceerd.

Na de resultaten van ons fylogenetische werk was het noodzakelijk om een nieuwe classificatie voor *Phyllanthus* en de nauw gerelateerde geslachten te creëren. Terwijl eerdere studies hadden voorgesteld om alles samen te voegen, besloten we *Phyllanthus* op te delen in kleinere groepen (hoofdstuk 8). Hiervoor werden de groepen *Cathetus*, *Cicca*, *Dendrophyllanthus*, *Emblica Kirganelia*, *Moeroris*, *Nellica* en *Nymphanthus* weer als aparte geslachten beschouwd en het ondergeslacht

Lysiandra werd ook als een aparte groep beschreven. Met deze indeling worden de geslachten *Glochidion*, *Breynia* en *Synostemon* behouden, terwijl er een classificatie wordt gecreëerd op basis van monofyletische groepen. Meer dan 600 soorten werden in deze nieuwe classificatie verplaatst van *Phyllanthus* naar een andere groep. Als *Glochidion* en de andere geslachten in *Phyllanthus* werden opgenomen, dan zou dit ook hebben geleid naar de overzetting voor 400 verschillende soorten. Verschillende parafyletische secties en ondergeslachten werden uitgebreid met de soorten die erin genesteld zijn. Beide oplossingen voor de parafylie van *Phyllanthus* zijn mogelijk, maar door het geslacht op te delen in kleinere groepen zoals hier voorgesteld, vinden we dat dit de evolutionaire geschiedenis van de groep beter weerspiegelt. In plaats van een gigantische groep met meer dan 1200 soorten, wordt er zo een onderscheid gemaakt tussen kleinere geslachten met een variabel aantal soorten van 20 tot 210 soorten.

Met behulp van de fylogenie uit hoofdstuk 5 hadden we eerder gekeken naar verschillende morfologische evolutionaire patronen, maar we wilden verder kijken hoe de hele stam Phyllantheae zo divers werd en hoe deze zich in de loop van de tijd verspreidde. Terwijl een breed gedefinieerd geslacht *Phyllanthus* voor zou komen in alle tropische gebieden op aarde, zijn de hier afgesplitste groepen vaak alleen aanwezig op een of twee continenten. In hoofdstuk 9 duiken we in de verspreidingsgeschiedenis en hoe de huidige distributie van verschillende groepen tot stand is gekomen. Hierbij wilden we ook kijken naar de diversificatie van verschillende groepen, omdat deze niet allemaal even soortenrijk. De verspreiding die we zien bij de Phyllantheae wordt meestal toegedragen aan een oorsprong ten tijde van het zuidelijke continent Gondwana. Onze resultaten toonden aan dat de Phyllantheae-stam waarschijnlijk is ontstaan tijdens het Laat-Paleoceen dichtbij het Paleoceen-Eocente Thermal Maximum (PETM). De geslachten *Nellica* en *Cathetus* duiden op een vroege uitwisseling van soorten tussen Afrika en Azië. *Nellica* is een kleinere groep soorten die op de stamboom zuster is van de rest van de soorten vroeger toegedragen aan *Phyllanthus*. Deze groep komt voor in Afrika, Azië en Noord-Amerika. Deze verdeling ten tijde van het PETM komt overeen met een mogelijke oorsprong in wat bekend staat als de boreale tropen. Dit was een tropisch regenwoud hoog op het noordelijk halfrond aan het eind van het Paleoceen dat zorgde voor een verbinding en makkelijkere uitwisseling tussen Europa en Noord Amerika en toen het na het PETM afkoelde, verspreidden veel planten zich naar het zuiden richting Afrika en zuidelijk Azië. Veel tropische groepen waaronder wellicht *Nellica* stierven daarna uit in Europa. Vondsten van fossiel pollen in Europa wijzen er ook op dat *Flueggea* uit de stam Phyllantheae (zustergroep van *Nellica* en de andere groepen) of een verwant geslacht daar destijds aanwezig was. Binnen clades/genera vonden we dat hun verspreiding vaak het resultaat is van een beperkt aantal verspreidingsgebeurtenissen. Vaak werd het grote aantal soorten voor sommige groepen verklaard door een bestuivingsmutualisme met kleine motjes. Zowel de plant als bestuiver zouden een co-diversificatie zijn ondergaan. Bij het bestuderen van verschuivingen in de diversificatiesnelheid binnen de stam, ontdekten we dat het onderlinge bestuivingsmutualisme in verschillende clades niet altijd gelijk staat met een toename in de soortsvorming. In sommige clades heeft dit niet geleid tot een hogere mate van diversificatie en dit wordt mogelijk (maar niet volledig) verklaard door een verschil in verspreidingsvectoren/mechanismen.

De evolutie van de stam Phyllantheae werd hier onderzocht in relatie tot zijn systematiek en verspreidingsgeschiedenis, maar zoals uiteengezet in hoofdstuk 10, zijn er nog genoeg onderwerpen om verder te onderzoeken. Toekomstige studies kunnen de evolutie van specifieke clades proberen te ontrafelen en hoe de verschillende soorten zich hebben aangepast aan verschillende omstandigheden en zo van elkaar zijn gaan verschillen. Vooral het bestuivingsmutualisme met motten die in verschillende clades aanwezig zijn, biedt een geweldige kans om te bestuderen hoe zowel bestuiver als plant opgesloten zitten in een evolutionaire strijd en hoe ze zich aan elkaar aanpassen. In dit proefschrift heb ik onze kennis van de fylogenie van *Phyllanthus* en zijn verwante geslachten uitgebreid. Daarbij probeerden we de taxonomie weer te baseren op monofylie met groepen die nog steeds morfologisch van elkaar te onderscheiden zijn. Hoewel deze classificatie in de toekomst weer kan veranderen, blijft de stam een interessante studiegroep.

Curriculum Vitae

Roderick Bouman was born on October 31st, 1991, in Hilversum, the Netherlands. He obtained his bachelor degree in Biology at the University of Utrecht in 2013 and worked for his thesis on the fluctuations in CO2 levels during the Dark Ages based on lake core samples from Germany. From 2013 to 2015 he studied in Leiden and graduated cum laude for his Masters in Biology with a specialization in Evolution, Biodiversity and Conservation. While studying for his masters degree, he pursued several of his research interests during two major research internship, one on fossil crinoids and the other on pollination of heathers (*Erica*) in South Africa. After his masters, he worked for a brief research project on the evolution of *Erica* at Naturalis and the University of Mainz supervised by Timo van der Niet and Mike Pirie.

Since 2015 he has been working on his PhD at the Hortus botanicus Leiden in collaboration with Naturalis Biodiversity Center under the supervision of Prof. Paul Keβler and Prof. Peter van Welzen. The focus of this project was the evolution, systematics and bioactivity of the plant genus *Phyllanthus*. The preliminary results of this study and the new classification of *Phyllanthus* were presented to several research groups and at the Flora Malesiana XI conference in Brunei in 2019. While finishing his thesis, he started in 2019 as a taxonomist for cultivated varieties of bulbiferous plants at the Royal General Bulbgrowers Association (KAVB) in Hillegom where he worked for 2.5 years and in November 2021 he has been appointed scientific collection manager at the Hortus botanicus Leiden.

List of Publications

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Acknowledgements

With working at so many different departments in Leiden, there are also so many people I wish to thank. Naturally I would like to thank everyone at the Hortus botanicus Leiden for welcoming me and making my time there so great. I especially want to thank my promoters Paul Keβler and Peter van Welzen for their guidance and long support with my PhD. From the botanical garden I would also like to express my gratitude to Hanneke who always invited me to all sorts of projects and activities at the garden and to Gerda for her critical questions.

Both at Naturalis Biodiversity Center and at the Institute Biology of Leiden I had so many people supporting me. The lab staff was always willing to help me and I would like to thank Arjen, Bertie-Joan, Elza, Frank, Marcel and Roland. Thanks also goes out to Young Choi and Kim and all the students at the Natural Products lab for introducing me to the world of metabolites. Esmee Winkel is gratefully acknowledged for the beautiful illustrations of the new species in this thesis.

A heartfelt thanks goes out to everyone who helped me while gathering material and data. The fieldwork was only made possible through the funding from the Alberta Mennega foundation and the help I received from Richard Saunders in Hong Kong, Richard Corlett in Xishuangbanna and Joeri Strijk in Guangxi.

When I first started, the National herbarium was still located in that isolated little corner of the city near the station of Leiden Lammenschans, but it was never boring due to the people there. I would like to thank Nicolien, Roxali, Marnel, Ron, Jan, Paul and Hiltje, Pieter, and Brigitta, Frits, Sylvia, Michael, the late Jan-Frits, Willem, Max and my office roommate the late Peter Hovenkamp for making my time there so enjoyable.

My thanks also goes out to my fellow friends and fellow PhD students Andres, Kevin, Panos, Werner, Lizzie, Hector, Vicky, Dewi, Nienke, Ryan, Le Qin, Deyi, Marcel, Mehrdad, Leon my old “herbarium crew” of Mega, Izu, Dul, Saroj, Renyong and Richa and everyone else. I also want to thank my wonderful students Janna, Gerry and Aninda for their valuable help with tackling these tiny-flowered plants.

To my dear friends from my hometown, Raymond, Emma, Darius and Rogier, thank you for listening to my ramblings and all your support. A special thanks goes to my girlfriend Eka Iskandar who always stood by me during happy and sad moments and who I could always invite to go out for a walk to distract ourselves. Finally, I would like to thank my parents and the rest of my family for their love and support while I was finishing my studies.

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