



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

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Key words

Euphorbiaceae
Macraea
new species
Phyllanthaceae
Phyllanthus
revision
species descriptions
taxonomy

Abstract Within the morphologically diverse pantropical genus *Phyllanthus*, many subgenera, sections and sub-sections 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.

Published on 25 October 2019

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. 2014) into *Phyllanthus* and creating a large monophyletic 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. 2014, 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* subg. *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 subg. *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) Art. 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 subg. *Macraea* as separate from subg. *Isocladius*, but with the exclusion of (former) sect. *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.

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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 distinguishing *Macraea* species from other *Phyllanthus* species. A few Philippine and Pacific species are here transferred to subg. *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 subg. *Macraea*, that are currently placed in other subgenera and sections.

Other subgenera and sections morphologically most similar to *Macraea* are *Phyllanthus* subg. *Phyllanthus* sect. *Lysiandra* (F.Muell.) G.L.Webster, *P.* subg. *Ceramanthus* (Hassk.) Jean F.Brunel, *P.* subg. *Betsileani* (Jean F.Brunel) Ralim. & Petra Hoffm., *P.* subg. *Isocladus* G.L.Webster p.p., *P.* subg. *Phyllanthus* sect. *Loxopodium* G.L.Webster, *P.* subg. *Isocladus* G.L.Webster sect. *Antipodanthus* G.L.Webster and *P.* subg. *Phyllanthus* sect. *Salviniopsis* Holm-Niels. ex Jean F.Brunel. Species of sect. *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* subg. *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* subg. *Betsileani*, formerly sect. *Praemacraea* of subg. *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 subg. *Betsileani* are found in Madagascar (Ralimanana & Hoffmann 2011). *Phyllanthus* subg. *Isocladus* is currently monotypic (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* subg. *Phyllanthus* sect. *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* subg. *Isocladus* sect. *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* subg. *Phyllanthus*

sect. *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 led 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 subg. *Macraea* over its entire distribution. The species included here were either already placed in subg. *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. 2011) 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 subg. *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 subg. *Isocladus* and subg. *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 subg. *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. womersleyi* 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 dehiscence longitudinally and latrorse with the filaments deflexed so that the anthers are horizontal.

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 subg. *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 (subg. *Betsileani*, which was so similar that it was formerly included in subg. *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 subg. *Macraea* were included, but mainly from Sri Lanka, New Caledonia and Australia. Species from Sri Lanka appeared to be sister to the rest of subg. *Macraea*, but no species from Africa or the Pacific were included.

TAXONOMIC TREATMENT

This study was performed at Naturalis Biodiversity Center (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), 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 used to provide a unique identifier, when a particular herbarium houses several duplicates of a type collection.

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

Phyllanthus subg. *Macraea* (Wight) Jean F.Brunel (1987) 293. — *Macraea* Wight (1852) 27. — *Phyllanthus* sect. *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, dehiscence 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 tetrahedri-form, persistent after dehiscence. *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

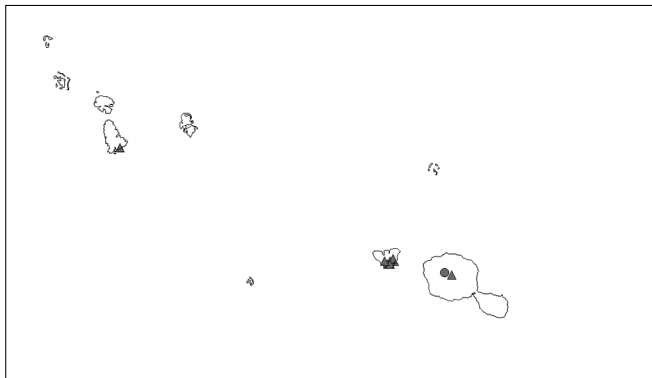
1. Stems barely branched, arising from a thick woody rhizome. Staminate disc glands often bell-shaped. — Africa 9. *P. glaucophyllus*
1. Stems usually branched several times, growing without a thick rhizome. Staminate disc glands flattened. — Outside Africa 2
2. Ovary on a gynophore. Stigmas united into 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 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 0.5–1 mm; stigmas c. 1 mm long. Fruits more than 2.2 mm 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 diam. Ovary verrucate 11. *P. macraei*
11. Staminate flowers 1–3 mm diam. Pistillate flower up to 3 mm 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 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 diam. Pistillate flowers 4–5.5 mm diam 22
21. Staminate flowers 0.7–1.7 mm diam. Pistillate flowers 1–3 mm diam 24
22. Leaf blades 3–37 by 2.5–18 mm. Staminate flowers 1.5–2.8 mm diam 8. *P. gardnerianus*
22. Leaf blades 7–80 by 4–32 mm. Staminate flowers 3–4 mm 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 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 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 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 diam. Pistillate pedicels 3–9 mm long, ovaries glabrous or verrucate 22. *P. virgatus*

1. *Phyllanthus aoraiensis* Nadeaud — Map 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 G, P (P00636871, P00636872)), 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 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



Map 1 Distribution of *Phyllanthus aoraiensis* Nadeaud (●) and *P. urceolatus* Baill. (▲) in French Polynesia.

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 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).

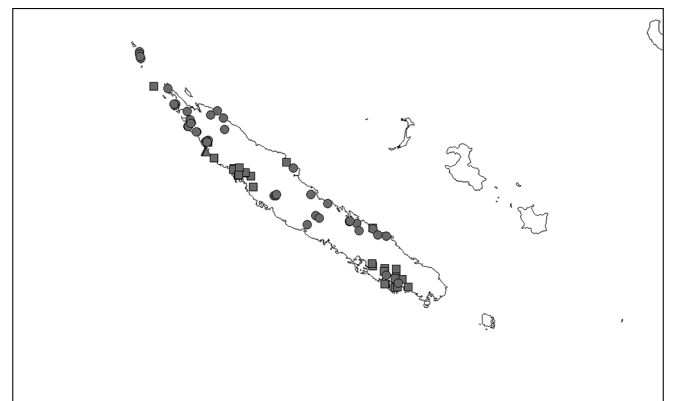
Note — A species morphologically very close to *P. urceolatus* and tentatively placed here in subg. *Macraea*. This species is endemic to Tahiti, but has not been collected since 1857 and is presumed extinct (Florence 1997, Wagner & Lorence 2011). *Phyllanthus aoraiensis* is easily distinguished from *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 2

Phyllanthus chrysanthus Baill. (1862a) 238; Müll.Arg. (1863) 34; (1866) 393; Guillaumin (1948) 177; Lohr.-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 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 subcylindrical, 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 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 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 diam; pedicel 1.5–2.5 mm long, glabrous; sepals 6,



Map 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.

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 diam, c. 0.1 mm high; ovary sessile, oblate(-ovoid), 0.6–1 mm 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 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 — Occurring in maquis shrubland, forests and near rivers, on rocky, alluvium, laterite and/or serpentine soils. Altitude: 0–1150 m. Flowering and fruiting all 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 long a. 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. *micrantheoides*

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 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 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 diam; stamens 0.5–0.7 mm long. *Pistillate flowers* c. 2 mm 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 diam, c. 0.1 mm high; ovary oblate-ovoid, c. 0.6 mm diam, c. 0.4 mm high; stigmas c. 1 mm long, bifid for 3/4 of the length. *Fruits* 2.2–3 mm 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 — Occurring 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: *HS 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 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 diam; stamens c. 0.8 mm long. *Pistillate flowers* c. 3 mm 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. — Lectotype (designated here): *J.F. Pancher 365* (P (P00066093); iso P (P00066094)), New Caledonia, Sommet du Pic. *Phyllanthus 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. *kafateensis* Guillaumin (1962) 247. — Lectotype (designated by Schmid 1991): *A. Guillaumin & M. Baumann 9657* (probably P, not seen), New Caledonia, Mont Kafate.

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 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 diam; stamens c. 0.5 mm long. *Pistillate flowers* c. 2.5 mm 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 diam, c. 0.1 mm high; ovary oblate, c. 1 mm diam, c. 0.8 mm high; stigmas 3, c. 1 mm long, bifid for 4/5 of the length. *Fruits* c. 2.2 mm 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 — Occurring 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 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. (2007) 483; P.T.Li & M.G.Gilbert (2008) 181; Chakrab. & N.P.Balakr. (2009) 527; (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 Catsuperr.

Phyllanthus simplex Retz. var. *tonkinensis* Beille (1927) 578. — Syntypes: *Balansa* s.n. (probably in P, not traced) Tonkin Cho-bo (black river), Vietnam; *Poila* 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 4–5 per side, barely visible above, clear underneath. *Staminate flowers* 1–3 together, 1.5–2.5 mm 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 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 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 diam, 0.2–0.3 mm high, smooth; ovary subglobose, c. 1 mm 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, stigmas and sepals persistent; 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 limestone ridges. Altitude: 900–2300 m. Flowering and fruiting all year round.

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

Notes — 1. This species is closely related to other species of subg. *Macraea* according to the phylogeny of Luo et al. (2011). Morphological characters such as its non-phyllanthoid branching and staminate flowers with free stamens confirm that this species should be placed in subg. *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 subg. *Macraea* with full certainty. *Phyllanthus 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* Buch.-Ham. ex D.Don and is also similar to *P. pseudo-parvifolius*. 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 <https://doi.org/10.15468/dl.uv7ddr>.

4. *Phyllanthus distichus* Hook. & Arn. — Map 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. forma *parvifolius* (Müll.Arg.) Wawra (1875) 149. — Type: *C. Gaudichaud-Beaupré* 289 (holo G-DC), USA, Hawai'i.

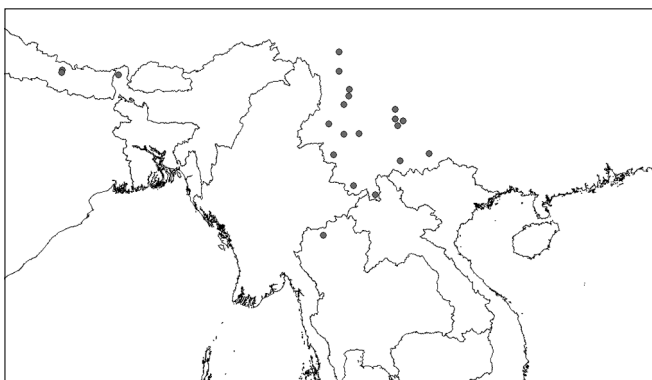
Phyllanthus sandwicensis Müll.Arg. var. *radicans* Müll.Arg. (1863) 32; (1866) 389. — Type: *C. Gaudichaud-Beaupré* s.n. (holo G-DC), USA, Hawai'i.

Phyllanthus sandwicensis Müll.Arg. f. *grandifolia* Wawra (1875) 149. — Type: *W. Hillebrand* 2340a (holo W), Hawai'i.

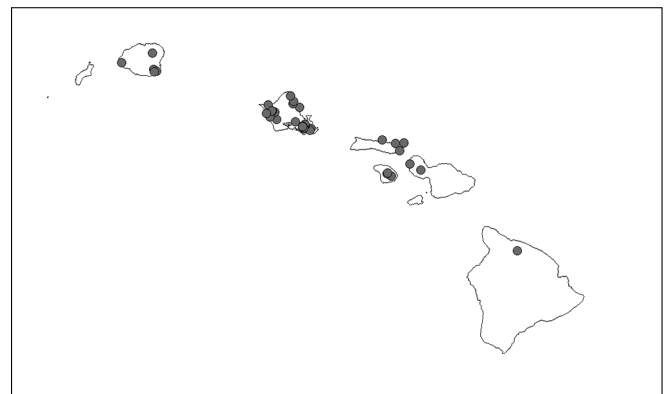
Phyllanthus sandwicensis Müll.Arg. f. *rufidus* Fosberg (1936) 6. — Type: *FR Fosberg* 12410 (holo BISH (BISH1009121); iso BISH (BISH1009120), CAS), USA, Hawai'i, Lanai, Haalelepaakai.

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*



Map 3 Distribution of *Phyllanthus clarkei* Hook.f. in SE Asia main land.



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

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 both sides, sage-green above, chestnut-brown underneath. *Staminate flowers* solitary to 7 together, c. 3 mm 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 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 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 diam, c. 0.1 mm thick; ovary sessile, globular-oblate, c. 1.5 mm 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 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 all year round.

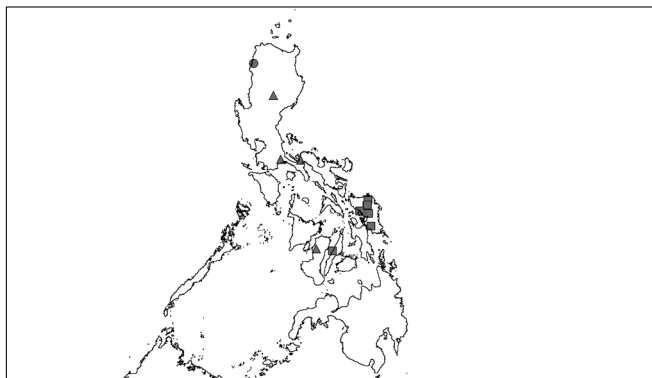
Notes — 1. This species is very variable in leaf shape and size. It can be distinguished by its size and robustness of the branches when compared to other species of subg. *Macraea*.

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 5

Phyllanthus dumosus C.B.Rob. (1909) 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.



Map 5 Distribution of *Phyllanthus dumosus* C.B.Rob. (●), *P. everettii* C.B.Rob. (▲) and *P. samarensis* Müll.Arg. (■) in the Philippines.

Stipules ovate-triangular, c. 0.4 by 0.2 mm, caducous, flat, membranous, margin thinner than centre, 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* 1–2 together, 0.7–0.8 mm 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 diam when closed, c. 3 mm 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 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 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 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 diam in bud, c. 2.5 mm 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 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 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 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 2/3 of the length. *Fruits* subglobose, 2.5–3 mm 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 Bisaya) (Merrill 1923).

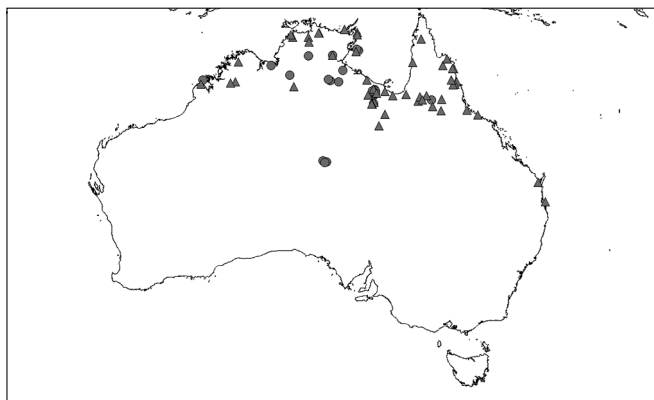
Note — Similar to some of the other species in the Philippines like *P. samarensis* and *P. lancifolius*. This species is distinct by its leaf blades, which are elliptic, as opposed to ovate in *P. lancifolius*, and larger than those found in *P. samarensis*. The resemblance with *P. samarensis* is quite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

7. *Phyllanthus exilis* S.Moore — Map 6

Phyllanthus exilis S.Moore (1926) 97; J.T.Hunter & J.J.Bruhl (1997) 153. — Type: GH 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 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 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 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 diam, flat; ovary sessile, subglobular, c. 1 mm 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 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).



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

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 7

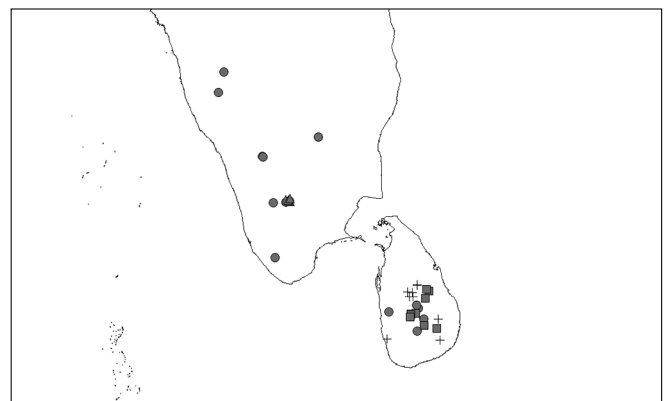
Phyllanthus gardnerianus (Wight) Baill. (1858) 628; Thwaites (1861) 282 (as *P. gardneri*); G.L.Webster (1997) 212; Chakrab. & N.P.Balakr. (2018) 300. — *Macraea gardneriana* Wight (1852) 27, pl. 1902-3. — *Phyllanthus simplex* Retz. var. *gardnerianus* (Wight) Müll.Arg. (1863) 33; (1866) 392; Hook.f. (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 GHK Thwaites C.P. 296 (K), Sri Lanka, Horton Plain.

Phyllanthus miquelianus Müll.Arg. (1863) 33; (1866) 391. — *Diasperum miquelianus* (Müll.Arg.) Kuntze (1891) 600. — Lectotype (designated here): RF Hohenacker 1130A (G-DC; iso L (L.2247451)), India.

Phyllanthus patens Miq. ex Müll.Arg. (1863) 34 (non *Phyllanthus patens* Roxb.). — Type: RF 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 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 diam; stamens 3, c. 1 mm long, filaments free, reflexed, thecae subovoid, c. 0.2 mm long. *Pistillate flowers* solitary, 4–5.5 mm 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 diam; ovary sessile, globular, 1–1.2 mm 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 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.



Map 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.

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).

Note — Very similar to *P. virgatus*, but with significantly larger pistillate flowers and often with wider leaves.

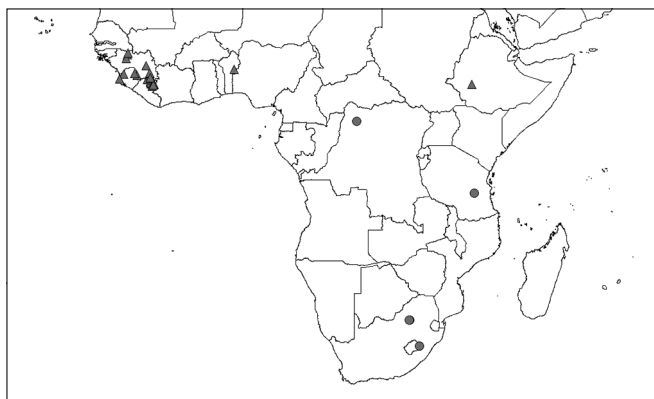
9. *Phyllanthus glaucophyllus* Sond. — Map 8

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. (1996) 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 (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. (in Brown et al. 1920) 395. — Lectotype (designated here): M.E. Barber 39 (K), South Africa, Kaffrarian 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 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 diam or bell-shaped, c. 0.2 mm diam, 0.2–0.3 mm high; stamens 3, 0.5–1 mm long, filaments free, thecae subglobose, 0.2–0.3 mm long. *Pistillate flowers* solitary, c. 2.5 mm diam; pedicel 6–10 mm long, glabrous; 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 diam; ovary globose-oblate, 1–1.5 mm diam, 0.5–1 mm high, glabrous; style absent, stigmas 3, c. 1 mm long, bifid for



Map 8 Distribution of *Phyllanthus glaucophyllus* Sond. var. *glaucophyllus* (●) and *P. glaucophyllus* var. *alpestris* (Beille) Verwijs (▲) in Africa.

2/3–3/4 of the length, reflexed. *Fruits* subglobose, 3–8 mm 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 all 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 subg. *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 diam a. var. *glaucophyllus*
1. Leaf blade discolorous. Staminate flowers 2–5 together; disc glands bell-shaped, 0.2–0.3 mm high. Pistillate pedicels c. 6 mm long. Fruits 6–8 mm 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 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 diam; pedicel c. 4 mm long; sepals obovate, c. 1 by 0.5 mm, white; disc glands circular, flat, c. 0.2 mm diam; stamens c. 0.5 mm long, thecae c. 0.3 mm long. *Pistillate flowers* solitary, c. 2 mm diam; 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 diam; ovary c. 1 mm diam, c. 0.5 mm high; stigmas bifid for 2/3 of the length. *Fruits* 3–4 mm 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. & stat. nov.

Phyllanthus alpestris Beille (1908) 56; N.E.Br., Hutch. & Prain (1912) 712; Hutch. & Dalziel (1928) 291; Jean F. Brunel (1987) 299; Essou (2006) 575. — Type: *AJB Chevalier 12907* (holo P), Guinea, Fouta Djallon.

Phyllanthus leonensis Hutch. (1917) 232; Hutch. & Dalziel (1928) 291. — Type: *NW Thomas 580* (holo K), Sierra Leone, Sendugu.

Phyllanthus monticola Hutch. & Dalziel (1928) 291. — Syntypes: *GF Scott-Elliot 5819* (K), Sierra Leone, near Regent; *GF Scott-Elliot 3962* (K); *CE 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 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 diam, 0.2–0.3 mm high; stamens c. 1 mm long, thecae 0.2–0.3 mm long. *Pistillate flowers* solitary or in pairs in usually upper axils, 1.5–2 mm 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 diam, covering $\pm$ 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 1/2 of the 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 — 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 all year round.

10. *Phyllanthus lancifolius* Merr. — Map 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. Edaña) 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 diam in bud, open 2–3 mm diam; pedicel 2–12 mm long, glabrous; sepals 6, ovate-elliptic, 1.2–1.6 by 0.6–0.8 mm, greenish to yellow-

ish white, midrib slightly curved inwards and thickened, apex rounded to acute, mucronate; disc glands 6, reniform, 0.1–0.4 mm 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 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 diam, covering $\pm$ 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 1/2 of the 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 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. everettii*).

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

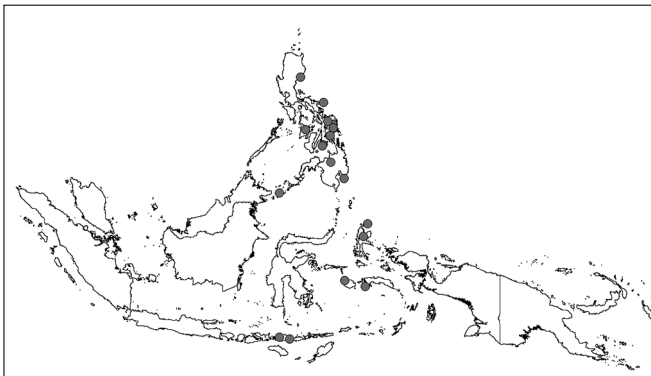
3. Merrill (1920) described *P. panayensis* as differing from *P. lancifolius* in its smaller leaves and longer pistillate pedicels. However, the leaf size is variable within individuals and specimens were found with leaves of the *P. panayensis* type but with longer pistillate pedicels (e.g., BS (Ramos) 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 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. rheedii* 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 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 diam, c. 0.1 mm high; stamens 3, c. 1 mm



Map 9 Distribution of *Phyllanthus lancifolius* Merr. in Malaysia.

long, filaments free, thecae subglobular, c. 0.3 mm long. *Pistillate flowers* solitary, 4–5 mm 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 diam; ovary sessile, globular, c. 1 mm 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 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 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 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 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 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 diam; ovary sessile, globular, c. 0.5 mm diam, c. 0.4 mm high, glabrous or verrucate; style absent, stigmas 3, c. 0.4 mm long, bifid for 1/2 of the length, reflexed. *Fruits* oblate, often splitting into 3 small, blunt tipped valves, 1–1.8 mm 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 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 (1997) 211; Chantar. (2005) 19; (2007) 493; N.P.Balacr. & Chakrab. (2007) 379; Chakrab. & N.P.Balacr. (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 1997): G. Gardner s.n. in GHK 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 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 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 diam; ovary sessile, globular, c. 0.5 mm diam, c. 0.5 mm high, glabrous; style absent, stigmas 3, c. 0.5 mm long, bifid for 1/2 of the length, reflexed. *Fruits* subglobular, c. 3 mm 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 distinguishable 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 10

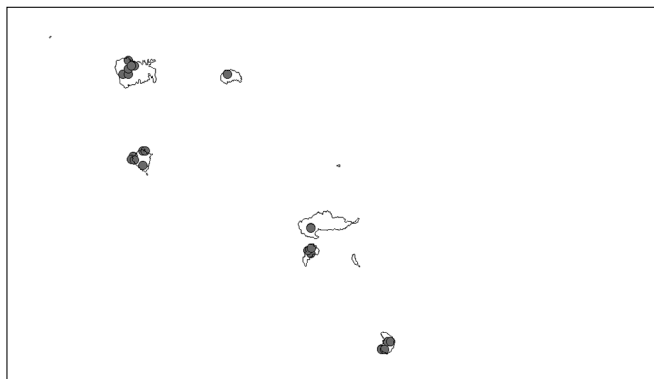
Phyllanthus pacificus Müll.Arg. (1863) 31; Drake (1892) 287; (1893) 180; F.Br. (1935) 137; J.Florence (1997) 129; W.L.Wagner & Lorence (2011) 82. — *Diasperus pacificus* (Müll.Arg.) Kuntze (1891) 600. — *Phyllanthus pacificus* Müll.Arg. var. *typicus* F.Br. (1935) 138, f. 21h, nom. inval. — Lectotype (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 (BISH1001662); iso BISH (BISH1001663)), 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), French Polynesia, Uahuka.

Phyllanthus pacificus Müll.Arg. var. *quaylei* F.Br. (1935) 139. — Type: *EH Quayle* 1341 (holo BISH), French Polynesia, Nuku Hiva.

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 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 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 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 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



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

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 stream-sides 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, mao on Nuku Hiva (Florence 1997).

Notes — 1. The placement in subg. *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

Phyllanthus prominulatus J.T.Hunter & J.J.Bruhl (1997) 153. — Type: *GM 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, septical, transversely ellipsoid and apically depressed, 0.8–0.9 mm long, 1.5–1.8 mm wide, yellow-brown, red-brown to green,

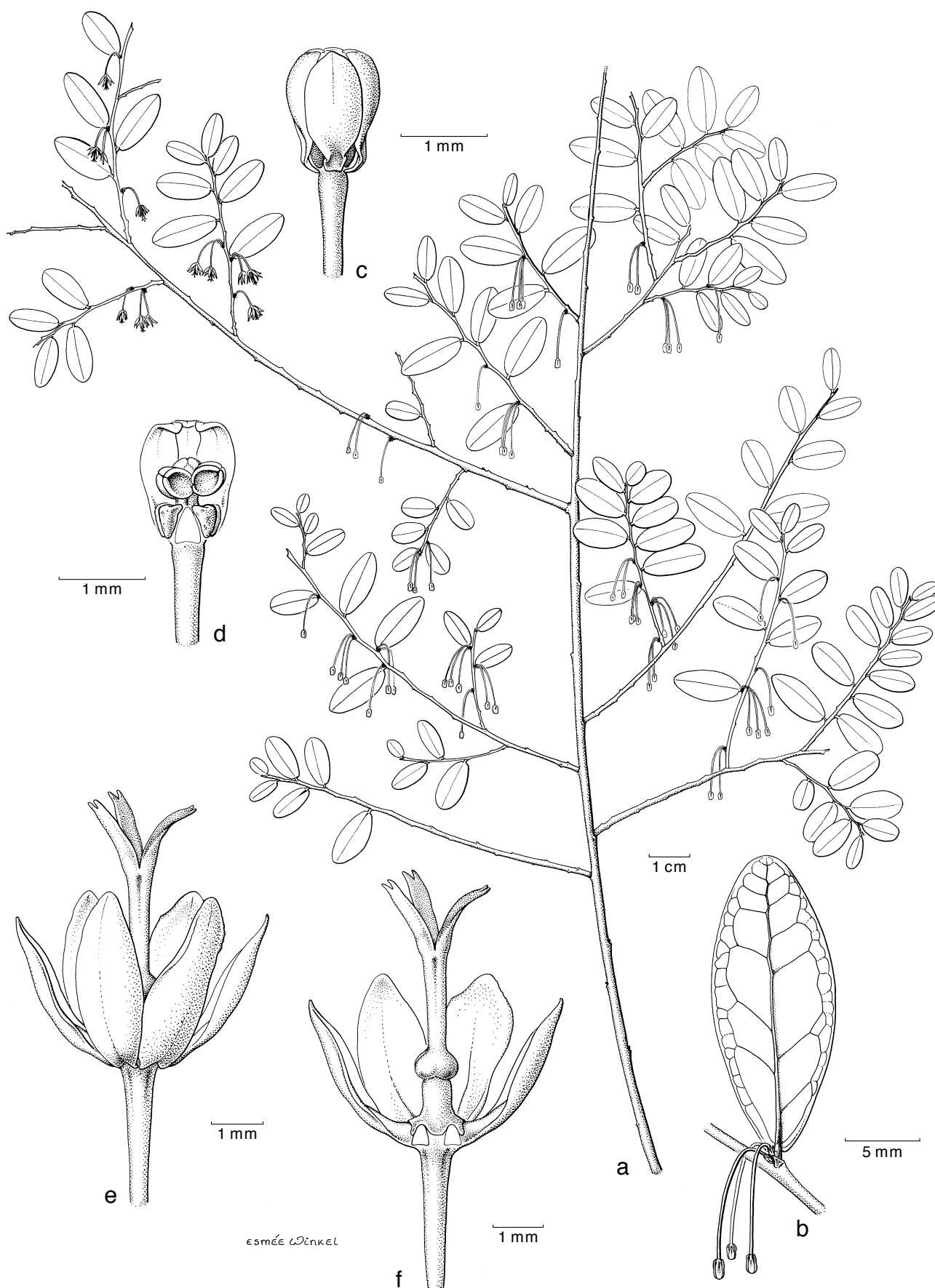


Fig. 1 *Phyllanthus ridsdalei* R.W.Bouman & Verwijs. a. Flowering branch drawn from herbarium specimen with hanging flowers; b. detail of staminate inflorescence; c. closed staminate flower; d. staminate flower (3 sepals removed); e. pistillate flower as seen when open, note the exserted style; f. pistillate flower (2 sepals removed), note the disc rim fused with the base of the gynophore (all: *CE Ridsdale 1479*, L). — Drawing by Esmee Winkel 2018.

cartilaginous, smooth, glabrous, grooved septically; 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 savannah 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. 1; Map 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: *CE 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 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 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.

Note — Pollen studied by Wu et al. (2016) showed that this species is part of subg. *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 below three elongated stigmas.

17. *Phyllanthus samarensis* Müll.Arg. — Map 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 diam; pedicel 2–10 mm long, glabrous, slender; sepals 6, ovate, c. 0.7 by 1 mm, green or white, apex obtuse; disc glands 6, oblate, c. 0.1 mm 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). *Pistillate flowers* solitary or in pairs, c. 2.5 mm 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 diam, flat; ovary sessile, globular, c. 0.8 mm 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 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, kaingin fields. Brown clay (loam) soil, often over limestone. Altitude: 366–650 m. Flowering and fruiting all year round.

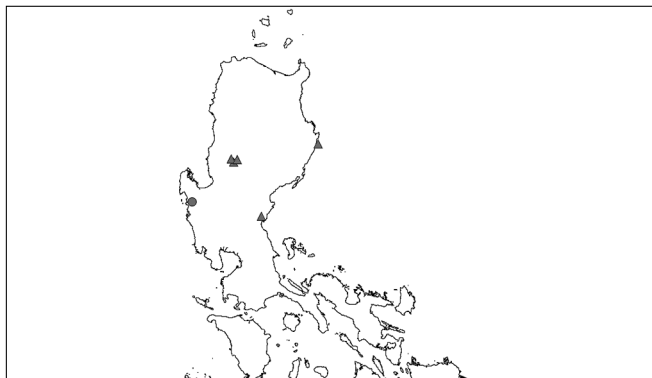
Vernacular name — Malaantagum (Samar-Leyte Bisaya; Merrill 1923).

Note — Similar to *P. myrtifolius*, but with densely tomentellous distal branches, slightly wider leaves and obtuse leaf base.

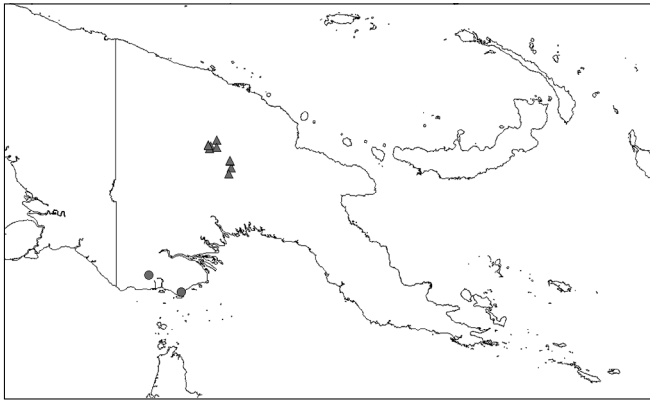
18. *Phyllanthus tararae* Verwijs, stat. & nom. nov. — Map 12

Phyllanthus virgatus G.Forst. var. *hirtellus* Airy Shaw (1980) 195 (non *P. hirtellus* F.Muell. ex Müll.Arg.). — Type: *LJ 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;



Map 11 Distribution of *Phyllanthus ridsdalei* R.W.Bouman & Verwijs (●) and *P. tenuipes* C.B.Rob. (▲) in the Philippines.



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

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 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 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 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 diam, flat; ovary sessile, globular, 0.8–1.2 mm 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 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 11

Phyllanthus tenuipes C.B.Rob. (1909) 78; Merr. (1923) 396. — Lectotype (designated here): *E.D. Merrill* 4419 (K; iso NY, US), 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 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, deflexed to horizontal position, thecae globose, c. 0.2 mm long, rounded. *Pistillate flowers* solitary or in pairs, axillary, 1.2–1.5 mm 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 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 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 (*CE Ridsdale ISU* 276).

20. *Phyllanthus urceolatus* Baill. — Map 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 (1891) 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 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 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 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 diam; ovary sessile, globular, c. 1 mm 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 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 — Recognizable by its large leaves with long pedicels.

21. *Phyllanthus ussuriensis* Rupr. & Maxim. — Map 13

Phyllanthus ussuriensis Rupr. & Maxim. (1857) 222; P.T.Li & M.G.Gilbert (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.

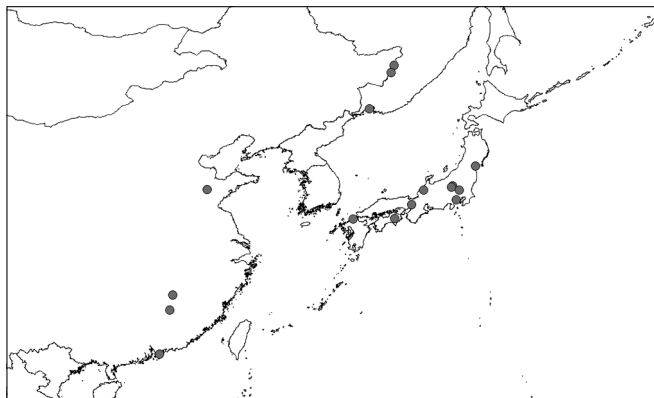
Phyllanthus simplex Retz. var. *chinensis* Müll.Arg. (1863) 33; (1866) 391. — *Phyllanthus virgatus* G.Forst. var. *chinensis* (Müll.Arg.) G.L.Webster (1971) 68. — Syntypes: *Park* 57 (G-DC), China, Canton; *Hance* 1223 (B, presumably lost), China, Hongkong; *C. Wilford* 66 (A), China, Hongkong.

Phyllanthus matsumurae Hayata ex Y.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 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 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 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 diam, c. 0.5 mm high, glabrous or verrucate; style very short, stigmas 3, c. 0.3 mm long, bifid for 1/2 of the length, reflexed. *Fruits* subglobular, 2–2.5 mm 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. Flowering: June to October.



Map 13 Distribution of *Phyllanthus ussuriensis* Rupr. & Maxim. in E Asia.

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).

Note — 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 vegetatively very similar *P. virgatus*, which has an annular disc in its pistillate flowers.

22. *Phyllanthus virgatus* G.Forst. — Map 14

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. (2007) 504; P.T.Li & M.G.Gilbert (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 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 & Hemsl. (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 (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, Tranquebar.

Phyllanthus anceps Vahl (1791) 95. — *Melanthesa anceps* (Vahl) Miq. (1859) 371. — Type: *Unknown collector s.n.* (holo C).

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 beckeri Müll.Arg. (1865) 74; Baill. (1865–1866) 341; (1866) 390; J.T.Hunter & J.J.Bruhl (1997) 157. — *Diasperus beckeri* (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. Vieillard 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 trachygynae Benth. (1873) 103; J.T.Hunter & J.J.Bruhl (1997) 157. — Lectotype (designated by Hunter & Bruhl 1997): *M. Schultz* 668 (K), Australia, Northern Territory, Port Darwin.

Phyllanthus weinlandii K.Schum. in K.Schum. & Lauterb. (1905) 287. — Syn-types: *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.

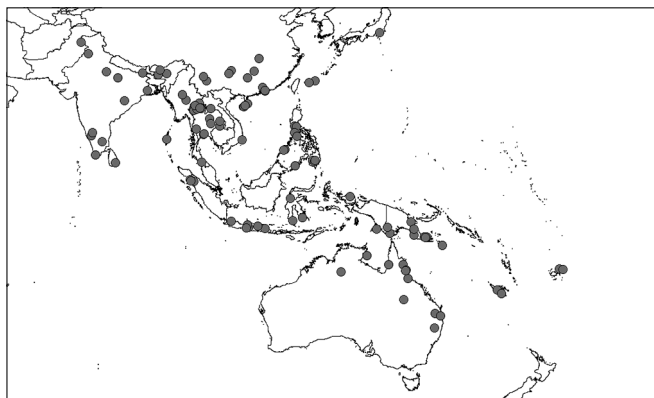
Phyllanthus narayanswamii Gamble (1925a) 329; (1925b) 902; N.P.Balakr. & Chakrab. (2007) 381; Chakrab. & N.P.Balakr. (2018) 349. — Lectotype (designated by Chakrabarty & Balakrishnan 2018): *V. Narayanswami* 640 (K; iso CAL, not seen), India, Dummakouda, Rampa hills, Godawari district.

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 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 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 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 diam; ovary sessile, globular, c. 0.8 mm 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.



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

Habitat & Ecology — Occurring 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, diarrhoea, dysentery, itch, gonorrhoea and (mammary) abscesses (Smith 1981, Quattrocchi 2016).

Vernacular name(s) — China: Huang zhu xi cao (Quattrocchi 2016). India: seed under leaf, virgate leaf-flower, bananauri, bhui-avali, bhuiavate, bhui-amla, biradi pello, bon baberi, jar amla, kaadu nelli, kadunelli, motibhuviali, niruri, tanda meral, uchchi usirika, uchhiyusirka (www.flowersofindia.net; Quattrocchi 2016). Myanmar: shit-sha (Kress et al. 2003). Thailand: khaang amphai, luuk tai bai, phaeng kham hoi (Quattrocchi 2016). Laos: ket 'hoy, 'khi doy (Quattrocchi 2016). Vietnam: v[aa]rjy [oos]e (Quattrocchi 2016). Indonesia: sahakèpo, sakahepo (Heyne 1950, Quattrocchi 2016). Philippines: kaya-an, kayut-bulan, kayut-bulang (Merrill 1923, Quattrocchi 2016). Tahiti: tei ni niu (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 specimens of *P. virgatus* in the prominent nervature on the lower side of the leaf blade.

23. *Phyllanthus wheeleri* G.L.Webster — Map 7

Phyllanthus wheeleri G.L.Webster (1995) 266; (1997) 215; Chakrab. & N.P.Balakr. (2018) 309. — Type: *LC 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 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 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 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 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* subglobose, 2–2.5 mm 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 subg. *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 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 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 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 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 diam, c. 0.1 mm high, foveolate; stamens 3, c. 0.9 mm long, filaments connate at base, reflexed, robust, thecae subglobose, c. 0.2 mm long, bright yellow. *Pistillate flowers* solitary, 2.5–3 mm 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 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 1/2 of the length, reflexed. *Fruits* subglobose, 2–2.5 mm 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 *Rhododendron* 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)).

Notes — 1. *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 exerted style) in that species are quite distinctive. They also do not overlap in distribution.

2. Placement in subg. *Macraea* was also confirmed by palynological studies by Punt (1980) and Wu et al. (2016), which found clypeate pollen typical for the group.

Acknowledgements The late 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.

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IDENTIFICATION LIST OF PHYLLANTHUS SPECIMENS

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|---|---|
| 1 = <i>Phyllanthus aoraiensis</i> Nadeaud | 11 = <i>Phyllanthus macraei</i> Müll.Arg. |
| 2a = <i>Phyllanthus chrysanthus</i> Baill. var. <i>chrysanthus</i> | 12 = <i>Phyllanthus minutiflorus</i> F.Muell. ex Müll.Arg. |
| 2b = <i>Phyllanthus chrysanthus</i> Baill. var. <i>deverdensis</i> M.Schmid | 13 = <i>Phyllanthus myrtifolius</i> (Moon ex Wight) Müll.Arg. |
| 2c = <i>Phyllanthus chrysanthus</i> Baill. var. <i>micrantheoides</i> (Baill.) M.Schmid | 14 = <i>Phyllanthus pacificus</i> Müll.Arg. |
| 3 = <i>Phyllanthus clarkei</i> Hook.f. | 15 = <i>Phyllanthus prominulatus</i> J.T.Hunter & J.J.Bruhl |
| 4 = <i>Phyllanthus distichus</i> Hook. & Arn. | 16 = <i>Phyllanthus ridsdalei</i> R.W.Bouman & Verwijs |
| 5 = <i>Phyllanthus dumosus</i> C.B.Rob. | 17 = <i>Phyllanthus samarensis</i> Müll.Arg. |
| 6 = <i>Phyllanthus everettii</i> C.B.Rob. | 18 = <i>Phyllanthus tararae</i> Verwijs |
| 7 = <i>Phyllanthus exilis</i> S.Moore | 19 = <i>Phyllanthus tenuipes</i> C.B.Rob. |
| 8 = <i>Phyllanthus gardnerianus</i> (Wight) Baill. | 20 = <i>Phyllanthus urceolatus</i> Baill. |
| 9a = <i>Phyllanthus glaucophyllus</i> Sond. var. <i>glaucophyllus</i> | 21 = <i>Phyllanthus ussuriensis</i> Rupr. & Maxim. |
| 9b = <i>Phyllanthus glaucophyllus</i> Sond. var. <i>alpestris</i> (Beille) Verwijs | 22 = <i>Phyllanthus virgatus</i> G.Forst. |
| 10 = <i>Phyllanthus lancifolius</i> Merr. | 23 = <i>Phyllanthus wheeleri</i> G.L.Webster |
| | 24 = <i>Phyllanthus womersleyi</i> Airy Shaw & G.L.Webster |
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