Taxonomic revision of *Phyllanthus* (Phyllanthaceae) in Madagascar and the Comoro Islands IV: subgenus *Anisonemoides* section *Pseudogomphidium* and *incertae sedis*

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Summary. This paper is the fourth part of the taxonomic revision of the genus *Phyllanthus* in Madagascar and the Comoro Islands. Here we treat *Pseudogomphidium* Ralim. & Cable sect. nov. consisting of nine species that we misplaced in the subgenus *Gomphidium* (Baill.) G.L.Webster in our previous paper. Two species are new to science: *Phyllanthus razakamalalae* Ralim. & Cable, sp. nov. and *P. ankirindrensis* Ralim. & Cable, sp. nov. We also treat three unplaced species: *P. analameræ* Leandri, *P. coluteoides* Müll.Arg. and *P. vergens* Baill. An identification key, descriptions, distribution maps and IUCN Red List assessments are provided.

Key Words. IUCN Red List, *Phyllanthus ankirindrensis*, *Phyllanthus razakamalalae*, taxonomy.

Introduction

Phyllanthus is one of the largest genera of plants known from Madagascar with 52 native species. It is often neglected by botanists because of complex taxonomy and difficulty in identifying species due to the small flowers.

The revision of Malagasy *Phyllanthus* by the lead author delimits nine other subgenera as detailed in three papers prior to this one (Ralimanana & Hoffmann 2011; Ralimanana *et al.* 2013, and Ralimanana & Hoffmann 2014). The first gave a general synopsis of the genus in the region and treated four subgenera in detail: *Isocladus* G.L.Webster, *Betsileani* (Jean F.Brunel) Ralim. & Petra Hoffm., *Kirganelia* (A.Juss.) G.L.Webster and *Tenellanthus* Jean F.Brunel (Ralimanana & Hoffmann 2011). The second paper treated subgenera: *Anisonemoides* (Jean F.Brunel) Ralim. & Petra Hoffm. and *Menarda* (Comm. ex A.Juss.) Ralim. & Petra Hoffm. (Ralimanana & Hoffmann 2014). The third paper dealt with subgenera: *Swartziani* (G.L.Webster) Ralim. & Petra Hoffm., *Afroswartziani* Ralim. & Petra Hoffm. and *Emblia* (Gaertn.) G.L.Webster (Ralimanana *et al.* 2013). This paper is the last in the series of the systematic revision of *Phyllanthus* L. in Madagascar and the Comoro Islands.

Phyllanthus is the most diverse genus in the family *Phyllanthaceae* (Hoffman *et al.* 2006). Floral characters are very important in species and subgenus identification, but species can be morphologically variable, and many characters are shared with closely related genera

(e.g. *Meineckia* Baill. and *Flueggea* Willd.). The generic delimitation of *Phyllanthus* has long been debated in the literature and classification of species remains a challenge. Presently *Phyllanthus* is broadly circumscribed to contain several segregate genera including *Glochidion* J.R.Forst. & G.Forst., *Breynia* J.R.Forst. & G.Forst. and *Sauropus* Blume, and is a member of tribe Phyllanthae Dumort. (Hoffmann *et al.* 2006), the largest and most difficult group in *Phyllanthaceae* sensu APG (Hoffmann & McPherson 2003; Hoffmann *et al.* 2006), formerly *Euphorbiaceae* subfamily *Phyllanthoideae*.

Some Malagasy *Phyllanthus* were originally described by Leandri (1934 – 1957) under *Glochidion*. In the *Flore de Madagascar et des Comores*, Leandri (1958) recognised seven species: *Glochidion ankaratrae* Leandri, *G. humbertii* Leandri, *G. lichenisilvae* Leandri, *G. marojejiensis* Leandri, *G. oreichtitum* Leandri, *G. perrieri* Leandri, and *G. sambiranensis* Leandri.

In his treatment of *Phyllanthus* of intertropical Africa, Brunel (1987) indicated the need to create a new section to accommodate the Malagasy *Glochidion* species sensu Leandri (1958), based on their pollen characters and floral morphology. After re-examination and study of specimens held in the Paris Herbarium and based on disc and seed characters, Hoffmann & McPherson (2003) moved these species to *Phyllanthus*. Although molecular research by Kathriarachchi *et al.* (2006) demonstrated that *Glochidion* is nested within *Phyllanthus*.

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Broad understanding of pollination biology of Phyllanthaceae was not known before the investigation of Kato *et al.* (2003), Kato & Kawakita (2017b) and Kawakita & Kato (2004a, b; 2009). Their results showed that some species belonging to subgenus *Gomphidium* are nocturnally pollinated by a species-specific *Epicephala* moth whose larvae feed on the seed, collected and transported pollen between flowers (Kawakita & Kato 2006; Kawakita & Kato 2009). Within the investigation of the origin of *Phyllanthaceae* - *Epicephala* mutualism, they reconstructed phylogeny for 46 species of Phyllanthaceae among them 22 *Epicephala*-pollinated including *Phyllanthus marojejiensis* (Leandri) Petra Hoffm. & McPherson and *P. humbertii* (Leandri) Petra Hoffm. & McPherson (both from Madagascar). This recent molecular analysis brought new updated information on the phylogenetic position of Madagascar *Phyllanthus* in respect to the species from New Caledonia, the centre of distribution of the subgenus *Gomphidium*. It showed that species pollinated by *Epicephala* were not monophyletic, the species from Madagascar are divergent from the clade containing the New Caledonian species and fall into a separate clade. Based on their findings, Kato & Kawakita (2017a) stated that *P. humbertii* and *P. marojejiensis* are closely related to subgenera *Betsileani* and *Anisonemoides*.

Subgenus *Betsileani* has non-phyllanthoid branching (all branches are equivalent), has three, entirely free stamens and pollen are perisyncoloprate. Entirely fused stamens of *Phyllanthus bernierianus* Baill. were noted as atypical of subgen. *Anisonemoides* (Ralimanana & Hoffmann 2014). However, the molecular data (Kathriarachchi *et al.* 2006) showed that *P. bernierianus* and *P. vakinankaratrae* Leandri (*Anisonemoides* with 5 – 6 free stamens) form a strongly supported clade (BP 99).

Morphologically the taxa treated here have phyllanthoid branching, 3 – 6 free or fused stamens and dehiscent fruits which are similar to the taxa in subgen. *Anisonemoides*. Brunel (1987) found that *Phyllanthus sambiranensis* Leandri and *P. oreichtitus* had both tricolporate pollen with macromicroreticulate exine which is similar to subgen. *Anisonemoides* (stephanocolporate pollen, rugulate exine in subgen. *Gomphidium* (Webster 1994)). Therefore, based on the morphological pattern, floral and pollen characters and genetic phylogeny, we here create a new section *Pseudogomphidium* Ralim. & Cable sect. nov. in subgen. *Anisonemoides* to accommodate the species grouped in subgen. *Gomphidium* sensu Ralimanana & Hoffmann (2011). It comprises ten species which are endemic to Madagascar and includes *P. bernierianus* treated in the previous paper. Two species *P. razakamalalae* Ralim. & Cable and *P. ankirindrensis* Ralim. & Cable are new to science and described in this paper.

We also present three unplaced species: *Phyllanthus analamerae* Leandri, *P. coluteoides* Baill. and *P. vergens* Baill.

Materials and Methods

This revision is based on herbarium material and field observations from throughout Madagascar. Herbarium specimens were examined at Kew (K), Paris (P) and in Madagascar (TAN and TEF). The descriptions are mostly based on dried specimens or softened plant parts from herbarium material. Distribution maps and conservation assessments were obtained using GIS (Arcview 3.3) and by applying IUCN criteria (IUCN 2012).

The floristic domains follow Humbert (1965). Information about habitat was obtained from field studies or from the field notes of other botanists.

Taxonomic treatment

1. ***Phyllanthus* subgen. *Anisonemoides*** (Jean F. Brunel) Ralim. & Petra Hoffm. sect. ***Pseudogomphidium*** Ralim. & Cable, sect. nov. Type: *Phyllanthus marojejiensis* (Leandri) Petra Hoffm. & McPherson.

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Monoecious *shrubs* or *subshrubs* with pinnatifid phyllanthoid branching (main branches with unlimited growth and leaves reduced to scales (cataphylls), the lateral (plagiotropic) with limited growth, deciduous, leafy and floriferous). Plagiotropic branches solitary. *Leaves* alternate. *Inflorescences* axillary, unisexual or bisexual cymes, 1 – 4-flowered. Tepals 5 (– 6). Disc glands free or absent in male flowers, lobed, extremely reduced or absent in female flowers. Stamens 3 – 5 (– 6); filaments free, partially or entirely fused into a column; anthers free or fused, oblong, basifixed, dehiscent longitudinally, apiculate or not apiculate; pollen tricolporate, macromicroreticulate exine. Ovary 3-locular, smooth or slightly rugose; styles free, deltoid, slightly bifid or entire; stigmas obtuse or acute. *Fruits* dehiscent; tepals persistent, sometimes accrescent in fruit; styles persistent; *seeds* 2 or sometimes 1 per locule, smooth or thinly striated longitudinally.

RECOGNITION. Section *Pseudogomphidium* is similar to subgen. *Gomphidium* sect. *Gomphidium* and subgen. *Anisonemoides* sect. *Anisonemoides* because of the phyllanthoid branching, disc glands in male flowers, and trilobular dehiscent fruits, but differs from sect. *Gomphidium* in the 5 (– 6) sepals (vs 6) and tricolporate pollen (vs trisyncolporate); differs from sect. *Anisonemoides* in the clustered bracts (vs not clustered),

the oblong anthers (vs globose or ovoid), relatively reduced or disc absent in female flowers (vs lobed),

the free, entire or slightly bifid style (vs fused and bifid).

Key to the species of *Phyllanthus* subgen. *Anisonemoides* sect. *Pseudogomphidium*

1. Petioles present 2
 Petioles absent 7
- 2(1). Leaf blades rounded to truncate at the base 3
 Leaf blades obtuse to attenuate at the base 4
- 3(2). Plagiotropic branches terete. Leaf blades acute at the apex. Inflorescence unisexual. Pedicels 6–9 mm in male flowers, 8–11 mm in female flowers. Disc glands absent in male flowers. Anthers apiculate. Female flowers 5–10 × 5–12 mm; tepals 6; ovary 5–7 × 4–6 mm. Fruits 6–8 × 7–8 mm, tepals in fruit 6–9 × 6.5–8 mm. Seeds thinly striated longitudinally 1. *P. ankirindrensis*
 Plagiotropic branches compressed. Leaf blades acuminate at the apex. Inflorescence bisexual. Pedicels 2–4 mm in male flowers, 18–25 mm in female flowers. Disc glands present in male flowers. Anthers not apiculate. Female flowers 1.5–2 × 1–1.5 mm; tepals 5; ovary 2–3 × 1.5–2 mm. Fruits 4–5 × 4–5 mm, tepals in fruits 1–2 × 0.5–1 mm. Seeds smooth 2. *P. humbertii*
- 4(3). Leaf blades obovate to oblong. Inflorescence bisexual or unisexual. Filaments entirely fused; anthers not apiculate. Female flowers 1–1.3 × 0.5–1 mm; ovary 0.8–1 × 0.8–1 mm. Fruits c. 2 × 1.8 mm. Seeds 1–1.2 × 0.7–1 3. *P. razakamalalae*
 Leaf blades ovate, elliptic, or subrhomboid. Inflorescence always unisexual. Filaments free or the inner fused up to $\frac{1}{3}$ their length; anthers apiculate. Female flowers 2–5 × 2–3.5 mm; ovary 1.7–2.6 × 1.7–2.6 mm. Fruits 2.8–4 × 3–4.5 mm. Seeds 1.8–2.5 × 1.7–2.4 mm 5
- 5(4). Plagiotropic branches pubescent. Bracts not clustered in male inflorescences. Stamens 6. Female flowers pedicels 7–20 mm long. Fruiting pedicels 8–20 mm long 4. *P. oreichtitus*
 Plagiotropic branches glabrous. Bracts in cluster of 3–6 mainly sterile bracts in male inflorescences. Stamens 5. Female flowers pedicels 2–5 mm long. Fruiting pedicels 2.4–5 mm long 6
- 6(5). Leaf blades symmetrical, flat; midvein flattened adaxially, prominent abaxially. Tepals 3–4 × 1.5–2 mm in male flowers, 4–5 × 2–5 mm in female flowers, and 4.2–5 × 2–5.3 mm in fruits 5. *P. perrieri*
 Leaf blades asymmetrical, margin revolute; midvein prominent adaxially and abaxially. Tepals 1.5–2.2 × 0.8–2 mm in male flowers, 2–2.2 × 1–1.2 mm in female flowers, and 2.2–2.8 × 1–1.2 mm in fruits 6. *P. sambiranensis*
- 7(1). Leaf blades spatulate falcate, 0.5–1.5 mm wide, concave abaxially; secondary veins indistinct adaxially and abaxially 7. *P. marojejiensis*
 Leaf blades 2.5–4.5 mm wide, flat; secondary veins flattened or prominent abaxially 8
- 8(7). Leaf blades subcoriaceous to coriaceous. Stamen with a central apiculum. Tepals 5, 2.8–3.5 × 1.4–1.6 mm in female flowers. Disc annular pentagonal. Ovary 1.8–2 × c. 2 mm 8. *P. lichenisilvae*
 Leaf blades membranous to chartaceous. Anthers not apiculate and different lengths. Tepals 6, 1.3–1.5 × 1–1.2 mm in female flowers. Disc minute or absent. Ovary 1–1.3 × 1–1.4 mm 9. *P. ankaratrae*

1. *Phyllanthus ankirindrensis* Ralim. & Cable, sp. nov.

Type: Madagascar. Toamasina, Maroantsetra, summit of Ankirindro massif, 15°18'08"S, 49°33'04"E, alt. 671 m, 1 Feb. 1999, Schatz 3916 (holotype P!; isotype MO).

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Monoecious shrubs, to 1.50 m high. Branching pinnatifid, orthotropic branches terete, glabrous. Cataphylls and cataphyllary stipules caducous. Plagiotropic branches solitary, terete, 6–12 cm long, 1–1.8 mm in diam., smooth, glabrous. Stipules caducous. Leaves 3–6 per branch. Internodes 5–17 mm long. Petioles terete, 2–3 × 1–1.5 mm, glabrous. Leaf blades ovate, 30–60 ×

20–30 mm, rounded to truncate at the base, acute at the apex, chartaceous to subcoriaceous, glabrous on both sides; midvein flattened adaxially, prominent abaxially; secondary veins 2–4 pairs, flattened adaxially, prominent abaxially. Inflorescence unisexual, consisting of one male or one female flower, male and female inflorescences on different branches. Bracts triangular, 0.7–1 × 0.5–0.7 mm, entire, glabrous. Male flowers 4–6 × 3–4 mm. Pedicels 6–9 × 0.4–1 mm, glabrous. Tepals 5, unequal, oblong, 3–5 × 2.5–4 mm, obtuse, coriaceous, glabrous on both sides, veins unbranched. Disc absent. Stamens 5, entirely fused into a column; column terete, widened at the base, 1.5–2 × 0.5–0.8 mm; anthers fused, oblong, apiculate, 1–1.5 × 0.2–0.4 mm. Female

flowers 5 – 10 × 5 – 12 mm. Pedicels 8 – 11 × 0.5 – 2 mm, glabrous. Tepals 6, unequal, on two whorls (outer smaller, inner bigger), ovate, 5 – 7 × 6 – 7 mm, rounded, subcoriaceous, glabrous on both sides, margin entire, veins branched. Disc absent or lobed, thin, 0.1 – 0.2 mm thick. Ovary 3-locular, ovoid, 5 – 7 × 4 – 6 mm, smooth or slightly rugose, glabrous. Styles free, deltoid, slightly bifid at the apex, c. 1 mm long; stigmas obtuse. *Fruits* ovoid, 6 – 8 × 7 – 8 mm, exocarp thick c. 2 mm; fruiting pedicels 8 – 11 × c. 2 mm, glabrous. Tepals persistent, accrescent, 6 – 9 × 6.5 – 8 mm; columella c. 2 – 3 mm. *Seeds* 2 – 4 × 2 mm, thinly striated longitudinally. Fig. 1.

RECOGNITION. *Phyllanthus ankirindrensis* is similar to *P. humbertii* by the presence of a petiole, leaf blades rounded to truncate at the base and the stamens fused into a column, but differs from *P. humbertii* by leaf blades acute at the apex (vs acuminate), the inflorescence unisexual (vs bisexual), the disc glands absent in male flower (vs present), the 5 stamens (vs 3), female flowers size, 5 – 10 × 5 – 11 mm (vs 1.5 – 2 × 1 – 1.5 mm), the 6 tepals (vs 5), the ovary 5 – 7 × 4 – 6 mm (vs 2 – 3 × 1.5 – 2 mm), the fruits ovoid (vs globose), 6 – 8 × 7 – 8 mm (vs 4 – 5 × 4 – 5 mm) and the size of tepals in fruit 6 – 9 × 6.5 – 8 mm (vs 1 – 2 × 0.5 – 1 mm).

DISTRIBUTION. Endemic to Madagascar. Eastern floristic domain. Map 1.

SPECIMENS EXAMINED. MADAGASCAR. Toamasina: Maroantsetra, sommet du massif d'Ankirindro, 15°17'37"S, 49°33'10"E, alt. 640 m, Jan. 2003, *Antilahimena et al.* 1668 (K, MO); Maroantsetra, Ambinanitelo, Marovovonana, 15°18'41"S, 49°25'28", alt. 981 m, Sept. 2004, *Antilahimena et al.* 2689 (K, MO); Maroantsetra, Makira, 15°18'11"S, 49°33'13.9"E, alt. 160 m, 20 May 2007, *Rakotonasolo et al.* 1117 (K, TAN); Maroantsetra, summit of Ankirindro massif, 15°18'08"S, 49°33'04"E, alt. 671 m, 1 Feb. 1999, *Schatz* 3916 (P, MO).

HABITAT. Open mid-elevation humid forests, altitude 640 – 981 m.

CONSERVATION STATUS. This species has an AOO of 12 km², and an EOO of 2.15 km². The two locations known are outside of protected areas, and the species is threatened by habitat loss due to forest logging and shifting agriculture. This species is rated as Endangered (EN B2ab(i,ii,iii)).

ETYMOLOGY. The species epithet is derived from the name of the place where the type was collected.

2. *Phyllanthus humbertii* (Leandri) Petra Hoffm. & McPherson (2003: 308). *Glochidion humbertii* Leandri (1957: 215). Type: Madagascar, Massif de Marojejy, à l'Ouest de la rivière Manantenina, forêt humide sur laterite et gneiss, alt. 1450 m, Dec. 1948, *Humbert* 22495 (holotype P!, isotype WAG).

Monoecious *shrubs* or sometimes *sarmentose shrubs*. Branching pinnatifid; orthotropic branches flattened, striate, glabrous. Cataphylls triangular, 1 – 1.3 × 0.6 – 1 mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, 1 – 1 × 0.6 – 1 mm, coriaceous, entire, glabrous. Plagiotropic branches solitary, compressed, 10 – 18 cm long, 1 – 1.5 mm diam., striate, glabrous. Stipules caducous or persistent, triangular, 0.4 – 0.7 × 0.2 – 0.3 mm, membranous, entire, glabrous. *Leaves* 7 – 11 per branch. Internodes 5 – 20.5 mm long. Petiole terete, 4 – 6 × 0.7 – 1 mm, glabrous. Leaf blades ovate, 25 – 80 × 14 – 45 mm, 1.8 × longer than wide, rounded to truncate at the base, acuminate at the apex, acumen 1 – 2 cm, chartaceous, glabrous on both sides; midvein prominent on both sides; secondary veins 2 – 4 pairs, prominent on both sides. *Inflorescence* bisexual, consisting of 1 – 4 male flowers and one female flower, or solitary female flower. Bracts triangular, 0.8 – 1 × 0.4 – 0.5 mm, entire or slightly erose, glabrous. Male flowers 2.7 – 4.3 × 1.8 – 2.6 mm. Pedicels 2 – 4 × 0.3 – 0.4 mm, glabrous. Tepals 5, unequal, oblong, 3 – 4 × 1.3 – 1.5 mm, round or obtuse, coriaceous, glabrous on both sides, margin entire, hyaline for 1/5 of entire tepal width on each side, veins unbranched. Disc glands 5, globose, c. 0.2 mm in diam. Stamens 3, entirely fused into a column; column terete, enlarged at the base, 1.3 – 3 × 0.6 – 0.8 mm; anthers fused, oblong, 0.7 – 1 × 0.3 mm, not apiculate. Female flowers 1.5 – 2 × 1 – 1.5 mm. Pedicels 18 – 25 × 0.4 – 0.5 mm, glabrous. Tepals 5, equal, ovate, 1 – 2 × c. 0.5 mm, obtuse, subcoriaceous, margin slightly erose, hyaline for 1/5 of entire tepal width, glabrous on both sides, veins unbranched. Disc extremely reduced or absent. Ovary 3-locular, ovoid, 2 – 3 × 1.5 – 2 mm, smooth, glabrous. Styles free, deltoid, entire, 0.4 – 0.5 mm long; stigmas obtuse. *Fruits* globose, 4 – 5 × 4 – 5 mm, glabrous; fruiting pedicels 20 – 27 × 0.5 – 0.7 mm, glabrous; tepals persistent, 1 – 2 × 0.5 – 1 mm; columella 2 – 2.8 × 0.5 – 0.6 mm. *Seeds* 2.5 – 3 × 1.5 – 2 mm, smooth.

DISTRIBUTION. Endemic to Madagascar. Central floristic domain. Map 2.

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Massif de Marojejy, à l'Ouest de la rivière Manantenina, forêt humide sur laterite et gneiss, alt. 1450 m, Dec. 1948, *Humbert* 22495 (P).

HABITAT. Open humid forests, altitude 1450 m.

CONSERVATION STATUS. *Phyllanthus humbertii* is known from two collections: the type and another specimen from Marojejy made by *Kawakita & Kato* 235 (KYO not seen). This species is probably very rare and its area of occupancy (AOO) is estimated to be less than 10 km². The species is threatened by

Fig. 1. *Phyllanthus ankirindensis* (G. E. Schatz 3916, P). A habit; B leaf; C female flower; D male flower. DRAWN BY R. L. ANDRIAMIARISOA.

Map 1. Distribution of *Phyllanthus ankirindrensis* in Madagascar.

Map 2. Distribution of *Phyllanthus humbertii* in Madagascar.

habitat loss due to illegal logging. It is therefore rated as Critically Endangered (CR B2ab(ii,iii,iv)).

3. *Phyllanthus razakamalalae* Ralim. & Cable, sp. nov.

Type: Madagascar. Antsiranana: Antomboka, Ambodimanga, Ambanja, 13°45'12"S, 048°31'19"E, alt. 41 m, 4 Dec. 2000, *Razakamalala et al.* 45bis (holotype K!; isotype MO).

<http://www.ipni.org/urn:lsid:ipni.org:names:77213111-1>

Monoecious *shrubs*, 0.5 – 1 m high. Branching pinnatifid; orthotropic branches terete, smooth or striate, glabrous. Cataphylls triangular, 0.4 – 0.7 × 0.3 – 0.4 mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, 0.3 – 0.5 × 0.3 – 0.4 mm, coriaceous, entire, glabrous. Plagiotropic branches solitary, terete, 15 – 24 cm long, 0.5 – 0.8 mm in diam., striate, glabrous or with thin hairs. Stipules persistent, triangular, 1 – 1.2 × 0.2 – 0.3 mm, membranous or chartaceous, entire, glabrous. *Leaves* 9 – 20 per branch. Internode 6 – 10 mm long. Petioles terete, 1 – 2 × 0.2 – 0.3 mm, glabrous. Leaf blades obovate to oblong, 12 – 40 × 7 – 11 mm, 1.7 – 3.6 × longer than wide, obtuse at the base, rounded sometimes with short apiculum 1 – 1.5 mm long at the apex,

membranous or chartaceous, glabrous on both sides; midvein flattened adaxially, prominent abaxially; secondary veins 3 – 5 pairs, flattened on both sides. *Inflorescences* bisexual or unisexual, consisting of 1 – 3 male flowers and one female flower or solitary female flower. Bracts triangular, 0.3 – 0.4 × 0.2 – 0.3 mm, entire, glabrous. Male flowers 2 – 2.5 × 1.8 – 2.5 mm. Pedicels 1 – 2 × 0.3 mm, glabrous. Tepals 5, unequal, oblong to elliptic, 1.5 – 2 × 0.5 – 0.8 mm, rounded or obtuse, coriaceous, glabrous on both sides, margin entire, hyaline for $\frac{1}{6}$ of total tepal width on each side, veins unbranched. Disc glands 5, globose, c. 0.2 × 0.2 mm. Stamens 5, entirely fused in column; column terete, 0.9 – 1.2 × 0.4 mm; anthers fused, oblong, not apiculate, c. 0.8 × 0.3 mm. Female flowers 1 – 1.3 × 0.5 – 1 mm. Pedicels c. 1 × 0.3 mm, glabrous. Tepals 5, subequal, oblong to elliptic, 0.7 – 1.3 × 0.4 – 0.5 mm, obtuse, coriaceous, glabrous on both sides, margin entire, hyaline for $\frac{1}{5}$ of entire tepal width on each side, veins unbranched. Disc lobed. Ovary 3-locular, ovoid or subglobose, 0.8 – 1 × 0.8 – 1 mm, smooth, glabrous. Styles free, deltoid, entire or slightly bifid at the apex, 0.5 – 0.7 mm long, stigmas obtuse. *Fruits* ovoid or subglobose, c. 2 × 1.8 mm, glabrous; fruiting pedicels c. 3 × 0.5 mm, glabrous; tepals 0.9 – 1.2 × 0.4 – 0.5 mm; columella 1 – 1.3 × 0.3 mm. *Seeds* 1 – 1.2 × 0.7 – 1 mm, thinly striated longitudinally. Fig. 2.

Fig. 2. *Phyllanthus razakamalalae* (C. Birkinshaw 1047, TAN). A habit; B leaf; C male flower; D stamens; E female flower. DRAWN BY R. L. ANDRIAMIARISOA.

RECOGNITION. *Phyllanthus razakamalalae* is similar to *P. humbertii* by the bracts not in a cluster, the filaments and anthers entirely fused, not apiculate, and the deltoid free styles. It differs from *P. humbertii* in the leaf blades obovate to oblong (vs ovate), obtuse at the base (vs rounded to truncate), rounded at the apex sometimes with a short apiculum (vs acuminate, acumen 1–2 cm long) and the 5 stamens (vs 3).

DISTRIBUTION. Endemic to Madagascar. Central floristic domain. Map 3.

PARATYPE: MADAGASCAR. Antsiranana: Reserve Naturelle Intégrale Tsaratanana, R. Ramena, 1–2 km SW of junction with R. Andilambe, 13°52'20"S, 048°50'50"E, alt. 547 m, 14 Nov. 2001, *Birkinshaw et al.* 1047 (MO, TAN).

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Réserve spéciale de Manongarivo, cours supérieur, 13°59'S, 48°26'E, alt. 700 m, 6 March 1999, *Gautier et al.* 3499 (G, K); Andapa, Doany Andranomololo, 14°21'34"S, 49°22'35"E, *Rakotovo et al.* 3199 (MO, TAN); Antomboka, Ambodimanga, Ambanja, 13°45'12"S, 048°31'19"E, alt. 41 m, 4 Dec. 2000, *Razakamalala et al.* 45bis (K, MO).

HABITAT. Margins of humid forest, altitude 700 m.

CONSERVATION STATUS. *Phyllanthus razakamalalae* has an AOO of 16 km² and an EOO of 2081.45 km². It is

known from four locations, two subpopulations are inside protected areas (Manongarivo and Tsaratanana). The subpopulations outside of the protected areas are threatened by habitat loss due to shifting agriculture, forest logging and annual fire. It is assessed as Endangered (EN B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv)).

ETYMOLOGY. The species epithet honours our colleague R. Razakamalala who collected the type specimen.

4. *Phyllanthus oreichtitus* Leandri (1935: 24). *Phyllanthus monticola* Leandri (1934: 450), **nom. illegit.** *Glochidion oreichtitum* (Leandri) Leandri (1937: 29). Type: Madagascar, Centre: Andringitra, forêt à mousses et sous-bois herbacé, at. 1800–2000 m, April 1921, *Perrier de la Bâthie* 13670 (lectotype P!, selected by Brunel (1987)).

Glochidion oreichtitum subsp. *tsaratanense* Leandri (1957: 217). Type: Madagascar, Centre-nord, mont Tsaratanana, alt. 2000 m, Oct. 1919, *Perrier de la Bâthie* 9714 (holotype P!).

Monoecious shrubs, 2–3 m high. Branching pinnatifid; orthotropic branches terete, 2.5–3 mm in diam., rugose or striate. Cataphylls triangular, 1.2–1.5 × 0.5–0.9 mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, c.1 × 0.7 mm, coriaceous, entire, glabrous. Plagiotropic branches solitary, terete or flattened toward the apex, 4–15 cm long, 1–1.4 mm in diam., pubescent. Stipules persistent, triangular, 1.8–2.5 × 0.5–0.8 mm, coriaceous, entire, glabrous. Leaves 8–22 per branch. Internodes 3–7 mm long. Petioles terete, c. 1 × 0.4–0.8 mm, glabrous. Leaf blades ovate, 4–40 × 7–16 mm, 0.5–2.5 × longer than wide, obtuse at the base, attenuate to acuminate at the apex, chartaceous, glabrous on both sides; midvein prominent on both sides; secondary veins 3–5 pairs, prominent on both sides. Inflorescences unisexual, solitary, male inflorescences and female inflorescences on different branches; bracts triangular or ovate, 0.5–0.8 × 0.2–0.3 mm, entire, glabrous. Male flowers 2.5–3 × 2–2.5 mm. Pedicels 3–7 × 0.3–0.4 mm, glabrous. Tepals 6, unequal, elliptic or oblong, 1.5–3 × 0.7–1 mm, round or obtuse, coriaceous, glabrous on both sides, margin entire, hyaline for 1/5 of tepals' width on each side, veins unbranched. Disc glands 6, globose or lenticular, 0.2–0.4 mm in diam. Stamens 6 in two whorls, the outer short free, the inner longer fused up to 1/3 their length, filaments terete or subangular, 0.8–2 × 0.4–0.7 mm; anthers free, oblong, apiculate, 0.6–0.9 × 0.2–0.3 mm. Female flowers 2.5–3 × 2.5–3 mm. Pedicels 7–20 × 0.4–0.5 mm, glabrous. Tepals 6, unequal, obovate or suborbicular, 2–3 × 1–1.5 mm, rounded, coriaceous, glabrous on both sides, margin entire, hyaline for 1/4 of tepal width on each side, veins

Map 3. Distribution of *Phyllanthus razakamalalae* in Madagascar.

unbranched. Disc lobed. Ovary 3-locular, globose, 2 – 2.6 × 1.8 – 2.6 mm, smooth or slightly rugose, glabrous. Styles 3, free, deltoid, entire or slightly bifid, 0.5 – 0.7 mm long; stigmas obtuse. *Fruits* depressed globose, 3 – 4 × 3.5 – 4.5

mm, glabrous; fruiting pedicels 7 – 20 × 0.4 – 0.5 mm; tepals persistent, 1.3 – 1.8 × 1.2 – 1.5 mm; columella c. 1.4 mm × 0.5 mm. *Seeds* c. 2 × 2.4 mm, smooth to thinly striated longitudinally. Fig. 3.

Fig. 3. *Phyllanthus oreichtitus* (J. Miller & P. B. Phillipson 3717, TAN). A habit; B leaf (abaxial surface); C leaf (adaxial surface); D tepal; E male flower; F stamens; G fruit. DRAWN BY R. L. ANDRIAMIARISOA.

DISTRIBUTION. Endemic to Madagascar. Central floristic domain. Map 4.

SPECIMENS EXAMINED. MADAGASCAR. Antananarivo: Centre-Est de Marovoay N of Moramanga, 1 Sept. 1958, *Capuron* 18783 (P); Ankazobe, 18°15'S, 47°9'E, alt. 850 m, 29 Nov. 1988, *Miller & Phillipson* 3717 (K, P). Antsiranana: Massif of Tsaratanana, alt. 2100 m, Nov. 1966, *Morat* 2258 (P); Ambanja, Marotaolana, massif of Tsaratanana, 14°09'19"S, 48°57'28"E, alt. 2063 m, 24 April 2001, *Rabenantoandro et al.* 506 (K, MO, TAN); Tsaratanana, Bealanana, Mangidrano, Montagne d'Ampitsinjovana, est campement lac Matsaborimaika, 14°08'53"S, 48°57'57"E, alt. 2275 m, 17 April 2003, *Reza et al.* 322 (MO, TAN). Fianarantsoa: Ialatsara, Ambohimahaso, 7 Feb. 1942, *Decary* 17474 (P); Ialatsara, Ambohimahaso, 7 Feb. 1942, *R. Decary* 17483 (P); Andringitra, forêt à mousses et sous-bois herbacé, at. 1800 – 2000 m, April 1921, *Perrier de la Bâthie* 13670 (P); Andringitra massif, alt. 1800 m, March 1922, *Perrier de la Bâthie* 14406 (P); Andranomainty, Ambalamanakana, 25 Feb. 1993, *Rabevohitra et al.* 2968R631 (TEF). Toamasina: Parc national Zahamena, Ihofika, South-East Manakambahiny, 17°39'13"S, 48°57'50"E, alt. 550 m, 22 Oct. 2002, *Randrianasolo* 328 (K, MO).

Map 4. Distribution of *Phyllanthus oreichtitus* in Madagascar.

HABITAT. Margin of humid forests, open humid forests. Altitude 850 – 2000 m.

CONSERVATION STATUS. *Phyllanthus oreichtitus* has an AOO of 32 km², and an EOO of 84305.72 km². Two subpopulations are found in the protected areas of Andringitra and Tsaratanana. This species is rated as Least Concern (LC).

NOTES. In his description Leandri (1957) recognised *Phyllanthus oreichtitus* subsp. *tsaratanensis*. He distinguished it from *P. oreichtitus* subsp. *oreichtitus* only by the leaf size and the fruiting pedicel length (smaller and shorter in *P. oreichtitus* subsp. *tsaratanensis*). We found no clear characters that distinguish between the two subspecies as well as a general overlap in all morphological characters. In our opinion there is no reason to differentiate two subspecies. In addition, *P. oreichtitus* has a large distribution area in Madagascar and is recorded in different types of habitat. The leaf size reduction is among of the usual adaptation characters in high altitude. In this treatment we put *Phyllanthus oreichtitus* subsp. *tsaratanensis* into synonymy.

5. *Phyllanthus perrieri* (Leandri) Petra Hoffm. & McPherson (2003: 308). *Glochidion perrieri* Leandri (1934: 606). Type: Madagascar, Massif of Manongarivo, alt. 800 – 1000 m, May 1909, *Humbert* 9918 (holotype P!).

Monoecious shrubs, 1 – 2 m high. Branching pinnatifid; orthotropic branches terete or angular toward the apex, rugose or striate, glabrous. Cataphylls triangular, 1.2 – 1.5 × 0.5 – 0.6 mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, 1 – 1.3 × 0.5 – 0.6 mm, coriaceous, entire, glabrous. Plagiotropic branches solitary, terete or becoming angular toward the apex, 7 – 20 cm long, 1 – 1.5 mm in diam., striate, glabrous. Stipules persistent or caducous, triangular, 0.6 – 1.3 × 0.4 – 0.6 mm, coriaceous, entire, glabrous. Leaves 9 – 13 per branch. Internodes 3 – 12 mm long. Petioles flattened, 1 – 1.5 × 0.8 – 1 mm, glabrous. Leaf blades ovate to elliptic, symmetrical, 9 – 45 × 7.5 – 22 mm, 1.2 – 1.8 × longer than wide, attenuate at the base, acute at the apex, flat, sub-coriaceous, glabrous on both sides; midvein flattened adaxially, prominent abaxially; secondary veins 3 – 5 pairs, branched at the margin, flattened adaxially, prominent abaxially. Inflorescences unisexual consisting of 1 – 2 male flowers or solitary female flower; male inflorescences and female inflorescences on different branches. Bracts triangular or obovate, in a cluster of 3 – 6 mainly sterile bracts in male inflorescence, 0.6 – 1 × 0.4 – 0.5 mm, entire or slightly erose, glabrous. Male flowers 3 – 4 × 2 – 3 mm. Pedicels 4 – 6 × 0.3 – 0.4 mm, glabrous. Tepals 5, unequal, ovate or oblong, 3 – 4 × 1.5 – 2 mm, round or

obtuse, coriaceous, glabrous on both sides, margin entire, hyaline for $\frac{1}{5}$ of entire tepal width on each side, veins branched. Disc glands 5, lenticular, c. 0.2 mm in diam. Stamens 5 entirely free; anthers free, oblong, apiculate, 0.5 – 0.7 × 0.2 – 0.3 mm. Female flowers 4 – 5 × 3 – 3.5 mm. Pedicels 2 – 2.4 × c. 0.5 mm, glabrous. Tepals 5, unequal, elliptic or obovate, 4 – 5 × 2 – 5 mm, obtuse, coriaceous, glabrous on both sides, margin entire, hyaline for $\frac{1}{6}$ of entire tepal width on each side, veins branched. Disc lobed. Ovary 3-locular, ovoid or globose, c. 2 × 1.7 – 2 mm, smooth, glabrous. Styles free, deltoid, entire, 1 – 1.5 mm long; stigmas obtuse. *Fruits* ovoid or globose, 3.5 – 4 × 3 – 4 mm, glabrous; fruiting pedicels 2.4 – 3 × 0.5 – 0.7 mm, glabrous; tepals persistent 4.2 – 5 × 2 – 5.3 mm; columella 1 – 1.2 × 0.5 – 0.6 mm. *Seeds* c. 2.5 × 1.7 mm, finely striated longitudinally.

DISTRIBUTION. Endemic to Madagascar. Sambirano floristic domain. Map 5.

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Tsaratanana, Antsaharatsy, Antsahabe, Mandrizavona, 13°47'56"S, 48°48'20"E, alt. 1300 m, 16 April 2000, *Antilahimena et al.* 480 (K, MO); Manongarivo, Bekolosy, 14°02'S, 48°18'E, alt. 1100 m, 24 Aug. 1994, *Dereleth* 117 (G, K, P); Manongarivo, Besinkara, Ambalafary, 14°04'S, 48°17'E, alt. 300 m, 14 July 1994, *Gautier &*

Chatelain 2326 (G, K, P); Massif of Manongarivo, alt. 800 – 1000 m, May 1909, *Humbert* 9918 (P); Manongarivo, 14°05'S, 48°20'E, alt. 1100 – 1200 m, 18 Oct. 1994, *McPherson & Werff* 16407 (MO); Manongarivo, Antsatrotro, 14°5'S, 48°22'E, alt. 1280 m, 30 Nov. 2000, *Wohlhausser et al.* 425 (G, K).

HABITAT. Margins of humid forest, altitude 250 – 1300 m.

CONSERVATION STATUS. *Phyllanthus perrieri* has an AOO of 24 km² and an EOO of 325.90 km². Two subpopulations are found inside of Manongarivo and Tsaratanana protected areas. The subpopulations found outside of the protected area are threatened by shifting agriculture. This species is therefore rated as Endangered (EN B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv)).

6. *Phyllanthus sambiranensis* Leandri (1934: 451). *Glochidion sambiranense* (Leandri) (1937: 29). Type: Madagascar. Haut bassin de Sambirano, 500 m, quartzite, Dec. 1912, *Perrier de la Bâthie* 9698 (lectotype P!, selected by Brunel (1987: 422)).

Glochidion sambiranense var. *trapezophyllum* Leandri (1958: 29), **nom. inval.**

Monoecious shrubs, 1 – 4 m high. Branching pinnatifid; orthotropic branches terete or angular toward the apex, striate, glabrous. Cataphylls triangular, 0.5 – 0.8 × 0.5 – 0.6 mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, 0.4 – 0.8 × 0.5 – 0.6 mm, coriaceous, entire, glabrous. Plagiotropic branches solitary, terete, 4.5 – 17 cm long, 0.5 – 1 mm in diam., striate glabrous. Stipules persistent, triangular, 0.4 – 0.6 × 0.3 – 0.4 mm, coriaceous, entire, glabrous. *Leaves* 9 – 51 per branch. Internodes 1 – 5 mm long. Petioles terete or flattened, 1 – 1.5 × 0.5 – 0.6 mm, glabrous. Leaf blades asymmetrical elliptic or obovate, 6 – 13 × 3 – 9 mm, 1.4 – 2 × longer than wide, cuneate to obtuse at the base, acute at the apex, coriaceous, revolute, glabrous on both sides; midvein prominent on both sides; secondary veins 3 – 4 pairs, prominent adaxially and abaxially. *Inflorescences* unisexual, solitary or fasciculate, consisting of 1 – 3 male flowers (1 developed and the others still in bud) or solitary female flower, male and female inflorescences on different branches. Bracts elliptic or obovate, in a cluster of 3 – 6 mainly sterile bracts in male inflorescences, 0.5 – 1 × 0.3 – 0.5 mm, entire, glabrous. Male flowers 2 – 2.5 × 1.7 – 2 mm. Pedicels 2 – 5 × c. 0.4 mm, glabrous. Tepals 5, unequal (2 outer smaller), oblong or obovate, 1.5 – 2.2 × 0.8 – 2 mm, round, coriaceous, glabrous on both sides, margins entire, hyaline for $\frac{1}{2}$ of tepal width on each side, veins unbranched. Disc glands 5, globose, c. 0.2 × 0.2 mm. Stamens 5, entirely free; filaments angular, 0.6 – 1 × c. 0.4 mm; anthers free, oblong, apiculate, 0.5 – 0.7 × 0.2 mm. Female flowers 2 – 2.5 × 2 – 2.5 mm. Pedicels 2.5 – 5 × 0.3 – 0.5 mm, glabrous. Tepals 5, subequal,

Map 5. Distribution of *Phyllanthus perrieri* in Madagascar.

oblong or ovate, 2 – 2.2 × 1 – 1.2 mm, obtuse, coriaceous, glabrous on both sides, margins entire, hyaline for $\frac{1}{6}$ of tepal width on each side, veins unbranched. Disc lobed. Ovary 3-locular, subglobose, 1.7 – 2 × 1.7 – 2 mm, smooth, glabrous. Styles entirely free, deltoid, entire, 0.4 – 0.6 mm long; stigmas obtuse. *Fruits* depressed globose, 2.8 – 3 × c. 3.5 mm, glabrous; fruiting pedicels 3 – 5 × 0.3 – 0.4 mm; tepals 2.2 – 2.8 × 1 – 1.2 mm; 1.3 – 1.6; columella c. 1.5 × 0.5 mm. *Seeds* 1.8 – 2 × c. 1.8 mm, smooth. Fig. 4.

DISTRIBUTION. Endemic to Madagascar. Eastern and Sambirano floristic domains. Map 6.

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Sambava, Analamaho, forêt de Makirovana, 14°10'52"S, 49°56'33"E, alt. 842 m, 22 Aug. 2007, *Andriamihajarivo et al.* 1301 (MO, P, TAN); Réserve Spéciale de Manongarivo, Mont Antsatrotro, 14°05'01"S, 048°23'18"E, alt. 1780 m, 14 Feb. 1994, *Andrianarisata et al.* 178 (MO); Ambatoharanana, Andranomena, Befandriana Nord, Makira, 15°07'58"S, 49°20'47"E, alt. 1164 m, 14 Feb. 2008, *Bernard* 801 (MO, P, TAN); Diana, 13°45'31"S, 048°05'27"E, alt. 456 m, 1 March 2011, *Bidault et al.* 27 (G, MO, P, TAN); Manongarivo, Besinkara, below Ambalafary, Anabotoaka, 14°04'S, 48°17'E, 8 April 1996, *Gautier* 3009 (G, TEF); East Ankaramy, summit ridge of Antsatrotro, Manongarivo, 14°05'S, 48°23'E, alt. 17750 – 1850 m, 11 April 1992, *Malcomber et al.* 1445 (MO, TAN); Sambava, Anjangoveratra, Anambofo, Makirovana, 14°09'35"S, 49°58'26"E, alt. 642, 11 March 2014, *Martial et al.* 578 (MO, P, TAN); Vohemar, Antsirabe-Nord, Andravinaambo, forêt d'Antsaolatra, 14°06'32"S, 49°57'34"E, alt. 666 m, 11 March 2014, *Martial et al.* 611 (MO, P, TAN); Manongarivo Massif, above village of Ambodisakoana, east of Ankaramy, 14°05'S, 48°20'E, alt. 1110 m, 16 Oct. 1994, *McPherson, & Werff* 16368 (MO, TAN); Manongarivo Massif, above village of Ambodisakoana, east of Ankaramy, 14°05'S 48°20'E, alt. 1110 – 1200 m, 18 Oct. 1994, *McPherson & Werff* 16401 (MO); Androranga, slope NE, alt. 1200 m, rocky, quartzites, *Perrier de la Bâthie* 9728; Manongarivo massif, alt. 1000 m, grès liassiques, *Perrier de la Bâthie* 9717 (P); Haut bassin de Sambirano, 500 m, quartzite, Dec. 1912, *Perrier de la Bâthie* 9698 (P); Antsiranana, Massif Tsaratanana, alt. 100 m, Jan. 1923, *Perrier de la Bathie* 15488 (P); Massif Tsaratanana, alt. 2000 m, April 1924, *Perrier de la Bathie* 16414bis (P); Manongarivo, by Andranomavo, 12 Aug. 2004, Manongarivo, East of Antsatrotro, 48°23'E, 14°05'S, alt. 1750 – 1850 m, *Malcomber et al.* 1445 (MO); Belinta, Kalobinono, 13°38'30"S, 48°39'48"E, alt. 492 m, 19 March 2009, *Rajaovelona et al.* 11 (K, TAN); Ambilobe, Manambato, Antsahavalany, 13°43'53"S, 49°23'38"E, alt. 1455 m, 27 Oct. 2007, *Randriambolomamonjy* 157 (MO); Between

Maromandia and Ambanja, 14°01'59.37"S, 48°09'14.46"E, alt. 127 m, 12 Sept. 2013, *Ralimanana* 1842 (K, TAN); Kalobinono, 13°38'23"S, 048°40'24"E, alt. 550 m, 28 Sept. 2013, *Randriatsivery & Manjato* 395 (G, MO, P, TAN); Galoko, 13°35'32"S, 048°42'36"E, alt. 125 m, 7 Oct. 2013, *Randriatsivery et al.* 450 (MO, P, TAN); Galoko, 13°36'11"S, 48°42' 37"E, alt. 430 m, 7 Oct. 2013, *Randriatsivery et al.* 477 (MO, P, TAN). Mahajanga: Analalava, Analantsoa, 14°2'44"S, 48°17'47"E, alt. 1135 m, 12 May 2014, *Onjalalaina et al.* 461 (K, TAN).

HABITAT. Margins of humid forests, open humid forests. Altitude 120 – 2000 m.

CONSERVATION STATUS. *Phyllanthus sambiranensis* has an EOO of 711268 km², it has 10 locations. Three subpopulations are found in protected areas (Manongarivo, Tsaratanana). The subpopulations outside of protected areas are threatened by habitat degradation due to shifting agriculture, illegal forest exploitation. It is therefore assessed as Vulnerable (VU Blab(i, iii, iv)).

7. *Phyllanthus marojejiensis* (Leandri) Petra Hoffm. & McPherson (2003: 308). *Glochidion marojejiense* Leandri (1957: 215). Type: Madagascar. Sommet Est du massif de Marojejy, Ouest de Manantenina, affluent de Lokoho, alt. 1850 – 2137 m, Dec. 1948, *Humbert* 22761 (lectotype P!, selected here). This collection is chosen as lectotype because of its good preservation and its richness in flowers and fruits.

Monoecious *shrubs* or *subshrubs*. Branching pinnatifid; orthotropic branches terete, rugose or striated, glabrous. Cataphylls triangular, 0.7 – 1.5 × 0.4 – 0.5 mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, 0.5 – 1.5 × 0.3 – 0.5, coriaceous, entire, glabrous. Plagiotropic branches solitary, terete, 1.5 – 5 cm long, 0.5 – 0.7 mm in diam., striate, glabrous. Stipules persistent, triangular or ovate, 0.8 – 1.5 × 0.3 – 0.5 mm, coriaceous, entire, glabrous, hyaline margin white. *Leaves* 23 – 45 per branch. Internodes 0.5 – 1 mm long. Petioles absent. Leaf blades spatulate falcate, asymmetrical, concave abaxially, 4 – 6 × 0.5 – 1.5 mm, 4.6 – 8 × longer than wide, attenuate at the base, rounded at the apex, coriaceous, revolute, glabrous on both sides; midvein flattened adaxially, prominent abaxially; secondary veins indistinct on both sides. *Inflorescences* unisexual, solitary, male inflorescences on proximal and female inflorescences on distal part of plagiotropic branches or different branches. Bracts elliptic, in a cluster of 5 – 7 mainly sterile bracts in male inflorescences, 0.4 × 0.3 mm, entire, glabrous. Male flowers 2 – 3.5 × 1.5 – 2 mm. Pedicels 0.5 – 1 × 0.3 – 0.5 mm, glabrous. Tepals 5, subequal, oblong, 2 – 3.5 × 1 – 1.6 mm, round,

Fig. 4. *Phyllanthus sambiranensis* (S. Malcomber et al. 1445, G. McPherson & H. van der Werff 16368, TAN). **A** habit; **B** leaf (adaxial surface); **C** leaf (abaxial surface); **D** branch with inflorescences; **E** male flower; **F** female flower. DRAWN BY R. L. ANDRIAMIARISOA.

Map 6. Distribution of *Phyllanthus sambiranensis* in Madagascar.

coriaceous, glabrous on both sides, margin entire, hyaline for $\frac{1}{5}$ of tepal width on each side, veins unbranched. Disc glands 5, lenticular, 0.2 – 0.3 mm in diam. Stamens 5, entirely fused into a column; column terete, 0.6 – 1.2 × 0.8 – 1 mm; anthers fused, elongate, apiculate, c. 1.2 × 0.2 – 3 mm. Female flowers 2.5 – 2.9 × 2.8 – 3 mm. Pedicels 0.5 – 0.8 × 0.4 – 0.5 mm, glabrous. Tepals 5, subequal, elliptic or obovate, 1.8 – 2.2 × 1 – 1.2 mm, round, subcoriaceous, glabrous on both sides, margin entire, hyaline for $\frac{1}{5}$ of tepal width on each side, veins unbranched. Disc alternitepalous lobed. Ovary 3-locular, globose, 1.5 – 2 × 1.5 – 2 mm, smooth, glabrous. Styles entirely free, deltoid, entire, 0.4 – 0.5 mm long; stigmas obtuse. *Fruits* (only young fruits seen) depressed globose, c. 2.8 × 3.2 mm; fruiting pedicels c. 2 × 0.5 mm; tepals 2 – 2.2 × 1 – 1.2 mm. Fig. 5.

DISTRIBUTION. Endemic to Madagascar. Eastern floristic domain. Map 7.

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Marojejy, track between campsite 2 and campsite 3, 14°25'41"S, 49°45'36"E, alt. 983 m, 9 Nov. 2010, *Andrinaivoravelona et al.* 378 (K, TAN); Loky Manambato, 13°12'18"S, 49°32'36"E, alt. 1099 m, 28 Nov. 2004, *Gautier et al.* 4776 (G, TEF); Sommet Est du

massif de Marojejy, Ouest de Manantenina, affluent de Lokoho, alt. 1850 – 2137 m, Dec. 1948, *Humbert* 22761 (P); Valley of Lokoho, Mont Beondroka, N of Maroambihy, alt. 1400 – 1450 m, *Humbert* 23608 (P, lectoparatype); valley of Ambatoharanana, bassin inférieur of Antsahaberoka, alt. 1600 – 1800 m, 15 – 25 Nov. 1959, *Humbert & Saboureaux* 31819 (P); Marojejy, N of Mandena, 14°26'S, 49°46'E, alt. 800 – 1300 m, 3 Dec. 1989, *Miller & Randrianasolo* 4656 (P); Marojejy, track to the summit, 14°26'32"S, 49°44'24"E, alt. 1585 m, 16 Oct. 2011, *Rakotoarinivo et al.* 588 (K, TAN); Marojejy Andapa, campement III, 11 Oct. 1988, *Rakotozafy & Raharilala* 2266 (TAN); Andapa, Marovato, 14°35'29"S, 49°39'15"E, alt. 710 m, 4 Feb. 2014, *Onjalalaina et al.* 254 (K, TAN); Marojejy summit, 14°26'57"S, 49°43'56"E, alt. 2145 m, 11 May 2015, *Rabarijaona et al.* 1021 (K, TAN); Marojejy, 14°25'33"S, 49°42'46"E, alt. 1510 m, 20 Nov. 2003, *Ranaivojaona* 565 (MO, TAN); Marojejy, 14°26'20"S, 49°42'15"E, 20 Nov. 2003, *Ranaivojaona* 568 (MO, TAN).

HABITAT. Margin of humid forests. Altitude 800 – 1510 m.

CONSERVATION STATUS. *Phyllanthus marojejiensis* has an AOO of 24 km², and an EOO of 838.21 km², two locations are known for this species and one of them is inside the Marojejy protected area. This species is threatened by habitat loss due to forest logging, illegal mining and annual fire. It is therefore rated as Endangered (EN B2ab(iii,v)).

8. *Phyllanthus lichenisilvae* (Leandri) Petra Hoffm. & McPherson (2003: 308). *Glochidion lichenisilvae* Leandri (1937: 29). Type: Madagascar. Mont Tsaratanana, 2000 m, silve à lichens, April 1921, *Perrier de la Bâthie* 16414 (holotype P!).

Monoecious *shrubs*, 3 – 4 m high. Branching pinnatifid; orthotropic branches terete, striate, glabrous. Cataphylls triangular, 0.8 – 1 × 0.3 – 0.5 mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, 0.5 – 0.8 × 0.3 – 0.5 mm, coriaceous, entire, glabrous. Plagiotropic branches solitary, terete or compressed, 3 – 8 cm long, 0.4 – 0.5 mm diam., striate, glabrous. Stipules persistent, triangular or subulate, 1 – 1.2 × 0.2 – 0.3 mm, coriaceous, entire, glabrous. *Leaves* 15 – 33 per branch. Internodes 1 – 3 mm long. Petioles absent. Leaf blades elliptic, asymmetrical, 4 – 7 × 2.5 – 3 mm, 1.6 – 2.3 × longer than wide, attenuate at the base, obtuse, acute or mucronulate at the apex, subcoriaceous to coriaceous, glabrous on both sides; midvein indistinct adaxially, prominent abaxially; secondary veins 3 – 4 pairs, flattened or invisible adaxially, prominent abaxially. *Inflorescences* unisexual, solitary, male inflorescences on proximal and female inflorescences on distal part of

Fig. 5. *Phyllanthus marojejiensis* (R. Ranaivojaona 565, TAN). A habit; B plagiotropic branch; C leaf (adaxial surface); D leaf (abaxial surface); E fruit; F male flower. DRAWN BY R. L. ANDRIAMIARISOA.

plagiotropic branches. Bracts triangular grouped in a cluster of 5 – 7 mainly sterile bracts in male inflorescences, elliptic, 0.5 – 0.6 × 0.4 mm, erose,

glabrous. Male flowers 1.5 – 2.3 × 1 – 1.5 mm. Pedicels 1.5 – 2 × 0.4 – 0.5 mm, glabrous. Tepals 5, subequal, oblong or obovate, 1.5 – 2.3 × 0.8 – 1.2 mm, round,

Map 7. Distribution of *Phyllanthus marojejiensis* in Madagascar.

coriaceous, glabrous on both sides, margins entire, hyaline for $\frac{1}{5}$ of tepal width on each side, veins branched. Disc glands 5, lenticular c. 0.2 mm in diam. Stamens 4 – 5 with a central apiculum (c. 1×0.3 mm), entirely fused into a column; column terete, c. 0.6×0.5 mm; anthers fused, elongate. Female flowers $2 - 3.5 \times 2.5 - 4$ mm. Pedicels c. 1.2×0.4 mm, glabrous. Tepals 5, unequal, obovate, $2.8 - 3.5 \times 1.4 - 1.6$ mm, obtuse, coriaceous, glabrous on both sides, margins entire, hyaline for $\frac{1}{6}$ of tepal width on each side, veins branched. Disc annular pentagonal. Ovary 3-locular, globose, $1.8 - 2 \times c. 2$ mm, smooth or slightly rugose, glabrous. Styles entirely free, deltoid, slightly bifid, $0.3 - 0.4$ mm long; stigmas obtuse. *Fruits* (only young fruits seen), globose.; tepals $2.8 - 3.5 \times 1.4 - 1.6$ mm.

DISTRIBUTION. Endemic to Madagascar. Central floristic domain. Map 8.

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Manongarivo, Bekolosy, $14^{\circ}02'S$, $48^{\circ}18'E$, alt. 1490 m, 16 Nov. 1994, *Gautier & Dereleth* 2568 (G, P); Marojejy massif, alt. 2000 – 2137 m, Nov. 1972, *Morat* 4074 (P); Mont Tsaratanana, 2000 m, silve à lichens, April 1921, *Perrier de la Bâthie* 16414 (P).

HABITAT. Margins of humid forests, open humid forests. Altitude 1490 – 2137 m.

Map 8. Distribution of *Phyllanthus lichenisilvae* in Madagascar.

CONSERVATION STATUS. *Phyllanthus lichenisilvae* has an EOO of 1804 km^2 , AOO of 12 km^2 and two locations in three protected areas (Manongarivo, Marojejy and Tsaratanana). It is rated as Endangered (EN B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv)).

9. *Phyllanthus ankaratrae* (Leandri) Petra Hoffm. & McPherson (2003: 308). *Glochidion ankaratrae* Leandri (1957: 214). Type: Madagascar. Environs Ambositra, forêt de Ranomena, July 1929, *Humbert & Swingle* 4845 (holotype P!).

Monoecious *shrubs*, c. 1 m high. Branching pinnatifid; orthotropic branches terete, rugose or striate, glabrous. Cataphylls triangular, $1 - 1.2 \times 0.4 - 0.5$ mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, $0.7 - 1 \times 0.3 - 0.5$ mm, coriaceous, entire, glabrous. Plagiotropic branches solitary or paired, terete or compressed, 3 – 9 cm long, $0.4 - 0.6$ mm in diam., striate, glabrous. Stipules persistent, triangular, $0.5 - 1 \times 0.2 - 0.3$ mm, slightly coriaceous, entire, glabrous. *Leaves* 12 – 33 per branch. Internodes 1 – 2.5 mm long. Petioles absent. Leaf blades elliptic to lanceolate, asymmetrical, $5 - 11 \times 2.5 - 4.5$ mm, 2 – 2.4 × longer than wide, attenuate at the base, acute at the

apex, membranous to chartaceous, glabrous on both sides; midvein prominent or flattened adaxially, prominent abaxially; secondary veins 3–5 pairs, indistinct adaxially, flattened or slightly prominent abaxially. *Inflorescences* unisexual, solitary, male inflorescences on proximal and female inflorescences on distal part of plagiotropic branches. Bracts triangular, in a cluster of 4–7 mainly sterile bracts in male inflorescences, obovate, $0.4 - 0.5 \times 0.2 - 0.4$ mm, slightly erose, glabrous. Male flowers $2 - 3 \times 2 - 2.5$ mm. Pedicels $1 - 1.3 \times 0.3 - 0.4$ mm, glabrous. Tepals 5, subequal, oblong or obovate, $2 - 3 \times 1 - 1.2$ mm, rounded, membranous, glabrous on both sides, margins entire, hyaline for $\frac{1}{6}$ of tepal width on each side, veins branched. Disc glands 5, lenticular, $0.1 - 0.2 \times 0.1 - 0.2$ mm. Stamens 3–5, entirely fused into a column; column terete, $0.6 - 1.3 \times 0.5 - 0.8$ mm; anthers fused, elongate, not apiculate, and with different lengths, $1 - 1.3 \times 0.2$ mm. Female flowers c. 1.5×1.5 mm. Pedicels $1 - 1.3 \times 0.4 - 0.5$ mm, glabrous. Tepals 6, subequal, elliptic or obovate, $1.3 - 1.5 \times 1 - 1.2$ mm, rounded, membranous, glabrous on both sides, margins entire, hyaline for $\frac{1}{6}$ of tepal width on each side, veins branched. Disc extremely reduced or absent. Ovary 3-locular, sub-globose, $1 - 1.3 \times 1 - 1.4$ mm, smooth, glabrous. Styles entirely free, deltoid, slightly bifid, $0.2 - 0.3$ mm high; stigmas obtuse. Fruits (only young fruits seen) sub-globose; tepals $1.4 - 1.5 \times 1 - 1.6$ mm. Fig. 6.

DISTRIBUTION. Endemic to Madagascar. Central floristic domain. Map 9.

SPECIMENS EXAMINED. MADAGASCAR. Antananarivo: track to Tsiazompaniry to Andapa, Ambohimadana Andramasina, June 1961, *Capuron* 20293SF (TEF); Fianarantsoa: Mont Tsaratanana, 2000 m, silve à lichens, April 1921, *Perrier de la Bathie* 16414 (P); Ambalavao, Ambalamanasy, Ambondrombe, $21^{\circ}51'S$ $047^{\circ}16'E$, 26 May 2004, *Rakotonasolo* 802 (MO, TAN).

HABITAT. Open humid forest, forest boundaries. Altitude 1300–1700 m.

CONSERVATION STATUS. *Phyllanthus ankaratrae* has an AOO of 12 km^2 , and an EOO of 4161.15 km^2 . Three locations and three subpopulations are known for this species. All of the subpopulations occur outside of protected areas. The species is threatened by habitat loss due to annual fire and forest logging and illegal mining. It is therefore assessed as Endangered (EN B1ab(iii, v) + 2ab(iii, v)).

2. Incertae sedis

1. *Phyllanthus analameræ* *Leandri* (1957: 225). Type: Madagascar. Antsiranana, plateau calcaire Analamera, Jan. 1938, *Humbert* 19151 (holotype P!).

Dioecious shrubs or a small tree, 1–2 m high. Branching pinnatifid; orthotropic branches compressed, rugose or flaky, glabrous. Cataphylls triangular, $1.8 - 2.5 \times 0.8 - 1$ mm, coriaceous, entire, glabrous. Cataphyllary stipules triangular, $1.5 - 2.5 \times 0.6 - 1$ mm, subcoriaceous, entire, glabrous. Brachyblasts terete ending by a cluster of 5–8 bracts, 5–10 mm long; bracts of brachyblast triangular, $1 - 2 \times 0.3 - 0.5$ mm, coriaceous, entire. Plagiotropic branches solitary or fascicled by two, terete, 1.5–8 cm long, $0.5 - 0.8$ mm in diam., pubescent. Stipules persistent, linear, $1 - 3 \times 0.2 - 0.4$ mm, membranous, entire, with hyaline margin, glabrous. Leaves 3–7 per branch. Internodes 3–10 mm long. Petioles terete, $1 - 2 \times 0.4 - 0.6$ mm, glabrous or pubescent. Leaf blades ovate, rarely elliptic, $10 - 32 \times 7 - 22$ mm, $1.4 - 1.5 \times$ longer than wide, obtuse to truncate at the base, obtuse to acute at the apex, chartaceous or membranous, glabrous on both sides or with thin hairs adaxially; midvein prominent on both sides, pubescent on upper side; secondary veins 2–3 pairs, flattened adaxially, slightly prominent abaxially. Male and female flower not seen. Information about female flowers deduced from fruit characters. Pedicels glabrous. Tepals 5, equal, obovate or oblong, subcoriaceous, glabrous, margins entire, hyaline for $\frac{1}{2}$ of tepal width on each side, veins unbranched. Disc lobed, $0.4 - 0.6$ mm thick, verrucose. Ovary 3-locular, globose or depressed globose, smooth, glabrous. Styles entirely free or fused at the base, bifid for $\frac{2}{3}$ their length, terete, 1–1.5 mm long; stigmas obtuse or acute. Fruits globose or depressed globose, $3 - 6 \times 4 - 8$ mm; fruiting pedicels $20 - 30 \times 0.3 - 0.4$ mm; tepals $1.6 - 2.5 \times 0.8 - 1.2$ mm; columella $2.5 - 4 \times 0.8 - 1$ mm. Seeds $1.7 - 1.9 \times 1.2 - 1.5$ mm, with about 10–20 thin undulating and longitudinal striae.

RECOGNITION. This species is similar to members of subgenus *Anisonemoides* by the capsular fruits but differs from them by the long brachyblasts (vs brachyblasts absent), the seed coat with undulating and longitudinal striae (vs thinly striated or smooth).

DISTRIBUTION. Endemic to Madagascar. Western floristic domain. Map 10.

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Ankarana, Tsingy, NE Mahamasina, $12^{\circ}50'47"S$, $49^{\circ}6'18"E$, alt. 82 m, 16 Jan. 2002, *De Block et al.* 1255 (BR, K, MO, TAN); plateau calcaire Analamera, Jan. 1938, *Humbert* 19151 (P). Mahajanga: Tsingy of Namoroka, $16^{\circ}27'S$, $45^{\circ}19'E$, alt. 140 m, 29 Sept. 1983, *Du Puy et al.* 383 (K, TAN); Ambilobe, Antsahatompy, Antsahatompy forest, $13^{\circ}37'05.4"S$, $50^{\circ}00'20"E$, alt. 96 m, 3 April 2013, *Ralimanana et al.* 1767 (K, MO, P, TAN).

HABITAT. Dry forests. Altitude 140 m.

Fig. 6. *Phyllanthus ankaratrae* (F. Rakotonasolo 802, TAN; SF 20293, TEF). A habit; B leaf (adaxial surface); C leaf (abaxial surface); D fruit; E male flower. DRAWN BY R. L. ANDRIAMIARISOA.

Map 9. Distribution of *Phyllanthus ankaratrae* in Madagascar.

CONSERVATION STATUS. *Phyllanthus analamerae* has an AOO of 16 km², four subpopulations are known for this species and two of them occur in Ankarana and Namoroka protected areas. The subpopulations outside of the protected areas are threatened by habitat loss due to mining exploitation and forest logging. It is therefore rated as Endangered (EN B2ab(ii,iii,iv)).

2. *Phyllanthus coluteoides* Müll. Arg. (Müller 1866: 335). Type: Madagascar. Antsiranana, Baie de Diego, Dec. 1848, *Boivin* 2664 (holotype P!).

Dioecious *shrubs*, 1 – 2 m high. Branching pinnatifid; orthotropic branches terete, rugose, glabrous. Cataphylls triangular, 1 – 1.2 × 0.5 mm, erose, glabrous. Cataphyllary stipules triangular, 0.7 – 1 × 0.5 mm, coriaceous, entire, glabrous. Brachyblasts terete, 6 – 9 mm long. Plagiotropic branches solitary or fascicled by 2, 4.5 – 9 cm long, 0.3 mm in diam., striate, glabrous. Stipules triangular or linear, 0.4 – 7 × 0.2 mm, coriaceous, erose, glabrous. *Leaves* 3 – 7 per branch. Internodes 2 – 5 mm long. Petioles terete, c. 1 × 0.3 mm, glabrous. Leaf blades suborbicular or ovate, 6 – 10 × 5 – 10.3 mm, 0.9 – 1.2 × longer than wide, rounded or obtuse at the base, rounded or obtuse at the apex,

Map 10. Distribution of *Phyllanthus analamerae* in Madagascar.

membranous, glabrous; midvein prominent on both sides, secondary veins 4 – 5 pairs, prominent on both sides. Male and female flowers not seen. Female flowers information derived from fruits characters. Bracts triangular, 0.7 × 0.4 mm, glabrous. Pedicels glabrous. Tepals 6, unequal, obovate, membranous, glabrous on both sides, veins branched. Disc lobed. Ovary 3-locular, globose, smooth, glabrous; styles, bifid for $\frac{1}{3}$ their length, fused at the base; stigmas obtuse or acute. *Fruits* depressed globose, 4 – 5 × 5 – 6 mm; fruiting pedicels 20 – 30 mm long; tepals c. 1.6 × 0.6 mm; columella 2 – 3 × 0.4 – 0.6 mm. *Seeds* 1.8 – 2.5 × 1.5 – 2 mm, smooth.

RECOGNITION. *Phyllanthus coluteoides* is similar to the members of subgenus *Anisonemoides* by the style bifid and fused at the base and the capsular fruit, the lack of male flower information makes the placement doubtful.

DISTRIBUTION. Endemic to Madagascar. Western floristic domain.

SPECIMENS EXAMINED. MADAGASCAR. Antsiranana: Baie de Diego, Dec. 1848, *Boivin* 2664 (P). Toliara: 26 Oct. 1940, *Decary* 16139 (P). Juan de Nova Island: Tsingy, 17°3'40"S, 42°43'29"E, alt. 5 m, 16 March 2013, *Hivert et al.* 546 (CBNM); *Perrier de la Bathie* 13788 (P).

HABITAT. Dry forest, thickets.

CONSERVATION STATUS. *Phyllanthus coluteoides* has a very restricted distribution and is known from three locations in the northern and south-western domains of Madagascar. The AOO is 12 km². Its habitat is declining due to fire, wood harvesting for charcoal production, conversion to pasture and agricultural activities. The three threatened locations are outside protected areas and are thought to be small and declining. This species is rated as Endangered (EN B2ab(ii, iii, iv)).

3. *Phyllanthus vergens* Baill. (Baillon 1892: 225). Type: Madagascar. Sambirano, station de Vavatohe, Feb. 1880, *Hildebrandt* 3328 (holotype P!; isotype, K!).

Apparently dioecious *shrubs* or *subshrubs*. Branching pinnatifid; orthotropic branches terete, rugose or striate, glabrous. Cataphylls triangular, 0.5 – 1 × 0.4 – 0.8 mm, coriaceous entire or erose, glabrous. Cataphyllary stipules triangular, 0.3 – 1 × 0.4 – 0.8 mm, coriaceous, entire, glabrous. Plagiotropic branches fasciculate by 2 – 4, terete, 4 – 10 cm long, 0.5 – 1 mm in diam., striate, glabrous. Stipules persistent or caducous, triangular, 0.3 – 0.4 × 0.2 – 0.3 mm, coriaceous, entire, glabrous. *Leaves* 5 – 12 per branch. Internodes 4 – 13 mm long. Petioles semiterete or flattened, 2 – 5 × 0.7 – 1 mm, glabrous. Leaf blades elliptic, 13 – 43 × 6 – 19 mm, 2.1 – 2.3 × longer than wide, attenuate at the base, acute at the apex, coriaceous, revolute, glabrous on both sides; midvein impressed adaxially, prominent abaxially; secondary veins 3 – 6 pairs, impressed adaxially, prominent abaxially. *Inflorescences* unisexual, consisting of 2 – 5 male flowers, on leafless branches borne at the base of plagiotropic branches. Bracts triangular, 0.2 – 0.4 × 0.2 – 0.3 mm, entire or erose, glabrous. Male flowers 0.8 – 1 mm high, 0.6 – 1 mm in diam. Pedicels 0.7 – 1 × 0.2 – 0.3 mm, glabrous. Tepals 5, unequal, elliptic, 0.7 – 1 × 0.4 – 0.6 mm, obtuse, coriaceous, margins entire, hyaline for $\frac{1}{3}$ – $\frac{1}{2}$ of tepal width on each side, glabrous on both sides, veins branched. Disc glands 5, globose, 0.1 – 0.2 × 0.1 – 0.2 mm. Stamens 3 (– 5), free; filaments terete, 0.4 – 0.6 × 0.1 – 0.2 mm; anthers free, ovoid, 0.1 – 0.2 mm long. Female flowers and fruit not seen.

DISTRIBUTION. Endemic to Madagascar. Sambirano floristic domain.

SPECIMENS EXAMINED. Species only known from the type.

HABITAT. Humid forest.

CONSERVATION STATUS. This species is only known from the 1892 type collection despite several expeditions to the area where it was collected. In addition, this area is seriously threatened by human activities such as habitat destruction by shifting agriculture. We believe that this species is very rare, and therefore it is rated as Critically endangered (CR B2ab(i, ii, iii, iv, v)).

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References

- Brunel, J. F. (1987). Sur le genre *Phyllanthus* L. et quelques genres voisins de la Tribu des Phyllanthaceae Dumort. (Euphorbiaceae, Phyllanthaceae) en Afrique intertropicale et à Madagascar. Thèse doctorale, Université Louis Pasteur, Strasbourg.
- Baillon, H. (1892). In: A. Grandidier, *Histoire Physique, Naturelle et politique de Madagascar* 2: 225. Paris.
- Hoffmann, P. & McPherson, G. (2003). Transfer of Madagascan *Glochidion* to *Phyllanthus*. *Novon* 13: 307 – 310.
- _____, Kathriarachchi, H. & Wurdack, K. J. (2006). A phylogenetic classification of Phyllanthaceae (Malpighiales; Euphorbiaceae sensu lato). *Kew Bull.* 61: 37 – 53.
- Humbert, H. (ed.) (1965). *Flore de Madagascar et des Comores, 111ème famille*. Firmin-Didot, Paris.

- IUCN (2012). *IUCN Red list Categories and Criteria : Version 3.1*, second edition. IUCN Species Survival Commission, Gland.
- Kathiriarachchi, H., Samuel, R., Hoffmann P., Mlinarec, J., Wurdack, K. J., Ralimanana, H., Stuessy, T. F. & Chase, M. W. (2006). Phylogenetics of tribe Phyllanthae (Phyllanthaceae; Euphorbiaceae sensu lato) based on nrITS and plastid *matK* DNA sequence data. *Amer. J. Bot.* 93 (4): 637 – 655.
- Kato, M., Takimura, A. & Kawakita, A. (2003). An obligate pollination mutualism and reciprocal diversification in the tree genus *Glochidion* (Euphorbiaceae). *Proc. Nat. Acad. Sci. USA* 100: 5264 – 5267.
- ____ & Kawakita, M. (2017a). Ecological research monograph. *Obligate pollination mutualism*. Springer, Japan.
- ____, & ____ (2017b). Biology of the obligate pollination Mutualism. In M. Kato & A. Kawakita (eds), *Obligate Pollination Mutualism*: p. 63 – 80. Springer, Japan.
- Kawakita, A. & Kato, M. (2004a). Evolution of obligate pollination mutualism in New Caledonian *Phyllanthus* (Euphorbiaceae). *Amer. J. Bot.* 91: 410 – 415.
- ____ & ____ (2004b). Obligate pollination mutualism in *Breynia* (Phyllanthaceae): further documentation of pollination mutualism involving *Epicephala* moths (Gracillariidae). *Amer. J. Bot.* 91: 1319 – 1325.
- ____, & ____ (2006). Assessment of the diversity and species specificity of the mutualistic association between *Epicephala* moths and *Glochidion* trees. *Molec. Ecol.* 15: 3567 – 3581.
- ____, & ____ (2009). Repeated independent evolution of obligate pollination mutualism in the *Phyllanthae-Epicephala* association. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 276: 417 – 426.
- Leandri, J. (1934). Espèces et localités nouvelles d'Euphorbiacées d'Afrique et Madagascar. *Bull. Soc. Bot. France* 81: 449 – 454.
- ____ (1935). *Catalogue des plantes de Madagascar, Euphorbiaceae*. G. Pitot & Cie, Académie Malgache, Tananarive.
- ____ (1937). Contribution à l'étude des Euphorbiacées de Madagascar. *Notul. Syst. Paris* 6: 11 – 35.
- ____ (1957). Notes systématiques sur les Euphorbiacées, *Phyllanthus* de Madagascar. *Mém. Inst. Sci. Madagascar* 8: 205 – 234.
- ____ (1958). *Euphorbiaceae I (Phyllanthoideae)*. In: H. Humbert (ed.), *Flore de Madagascar et des Comores, 111ème famille*. Firmin-Didot, Paris.
- Müller, J. (1866). Euphorbiaceae. In: A. De Candolle (ed.), *Prodromus Systematis Naturalis Regni Vegetabilis* 15 (2): 189 – 1286. Victor Masson, Paris.
- Ralimanana, H. & Hoffmann, P. (2011). Taxonomic revision of *Phyllanthus* (Phyllanthaceae) in Madagascar and the Comoro Islands I: synopsis and subgenera *Isocladus*, *Betsileani*, *Kirganelia* and *Tenellanthus*. *Kew Bull.* 66: 331 – 365.
- ____, ____ & Rajeriarison, C. (2013). Taxonomic revision of *Phyllanthus* (Phyllanthaceae) in Madagascar and the Comoro Islands III: subgenera *Swartziani*, *Afroswartziani* and *Emblica*. *Kew Bull.* 68: 535 – 558.
- ____ & ____ (2014). Taxonomic revision of *Phyllanthus* (Phyllanthaceae) in Madagascar and the Comoro Islands II: subgenera *Anisonemoides* (Jean F. Brunel) Ralim. & Petra Hoffm., stat. nov and *Menarda* Comm. ex A. Juss.) Ralim. & Petra Hoffm., stat. nov. *Adansonia* sér. 3, 36 (2): 265 – 301.
- Webster, G. L. (1994). Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Ann. Missouri Bot. Gard.* 81 (1): 33 – 144.

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