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Source: Systematic Botany, 49(1) : 192-208

Published By: The American Society of Plant Taxonomists

URL: https://doi.org/10.1600/036364424X17110456120767

Systematic Botany (2024), 49(1): pp. 192–208
ISSN 0363-6445 (print); ISSN 1548-2324 (online)

DOI 10.1600/036364424X17110456120767
Date of publication May 6, 2024

Three Unusual New Species of *Plukenetia* (Euphorbiaceae) from Madagascar: Species Radiation and Convergent Evolution in *P.* sect. *Madagascarienses*

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Abstract—We describe three unusual new species of *Plukenetia* sect. *Madagascarienses* from eastern Madagascar based on morphology, pollen, and molecular data. *Plukenetia analameranensis* is unusual in the genus and section for its flat androecium of sessile anthers on a flat receptacle and is most similar to *P. ankaranensis* sharing obovoid stylar columns. *Plukenetia antilahimenae* and *P. randrianaivoi* are distinct in sect. *Madagascarienses* and among palaeotropical species for their elliptic or obovate-elliptic, pinnately veined leaf blades. They differ primarily in indumentum characters, including stems and inflorescence axes pubescent versus glabrous, and stipule size. Pollen of the new species (unknown in *P. randrianaivoi*) have reticulate or finely reticulate exines, while that of *P. ankaranensis* has a rugulate exine; this pollen morphology contrasts with that of all other palaeotropical species, which have foveolate exines. Phylogenetic analysis of nuclear ribosomal ETS and ITS data show that *P. randrianaivoi* is firmly embedded in the sect. *Madagascarienses* clade and sister to *P. ankaranensis* (the other two new species could not be sequenced). Based on these molecular and pollen results, together with floral characters (most importantly completely connate styles), we suggest that the three new species and *P. ankaranensis* form a subclade, sister to the other two Malagasy species, *P. decidua* and *P. madagascariensis*. With the description of these three new species, sect. *Madagascarienses* (6 spp.) becomes substantially more diverse morphologically. This species radiation in Madagascar resulted in the independent evolution of several leaf and pollen characters that previously were thought to distinguish the two major clades of *Plukenetia*, specifically pinnately veined leaf blades and reticulate pollen that look remarkably similar to the leaves and pollen of the neotropical pinnately veined clade. An emended description of section *Madagascarienses*, a key to the species of sect. *Madagascarienses*, and an updated key to the sections of *Plukenetia* are provided.

Keywords—Acalyphoideae, leaf architecture, phylogeny, Plukenetieae, pollen, taxonomy

Plukenetia L. is a pantropical genus of vines, lianas, and perennial herbs belonging to tribe Plukenetieae in subfamily Acalyphoideae (Euphorbiaceae). The genus may be distinguished by its 4-carpellate ovary and fruits, and pair of extrafloral nectaries at the base of the adaxial leaf blade (Gillespie 1993, 2007; Cardinal-McTeague and Gillespie 2020). Several species are cultivated and/or wild-harvested for their edible seeds that are rich in omega-3 and omega-6 polyunsaturated fatty acids, including *P. conophora* (African walnut) in Africa (Akintayo and Bayer 2002; Amusa et al. 2014) and *P. carolis-vegae* Bussmann, Paniagua & C.Téllez, *P.* ×*huayllabambana* Bussmann, C.Téllez & A.Glenn, and *P. volubilis* L. (Sacha Inchi, Inca peanut) in the Neotropics (Bussmann et al. 2013; Kodahl and Sørensen 2021; Kodahl et al. 2022).

Plukenetia was most recently revised by Gillespie (1993, 2007), with additional neotropical (Jiménez 1993; Bussmann et al. 2009, 2013; Cardinal-McTeague and Gillespie 2020) and palaeotropical species (Gillespie 2023) described subsequently. Cardinal-McTeague and Gillespie (2020) proposed a revised sectional classification of the genus consisting of six sections, with 25 recognized species. This new classification was strongly supported by recent phylogenetic studies (Cardinal-McTeague and Gillespie 2016, 2020; Cardinal-McTeague et al. 2019). The genus comprises two main clades, a neotropical pinnately veined clade (*P.* sect. *Fragariopsis* (A.St.-Hil.) Card.-McTeag. & L.J.Gillespie [subclade P1] + *P.* sect. *Penninerviae* Card.-McTeag. & L.J.Gillespie [P2]) and a palmately veined clade, a division also supported by pollen morphology (tectum coarsely reticulate versus foveolate). The palmately veined clade is subdivided into a neotropical clade (*P.* sect. *Plukenetia* [P3]) and a strongly supported but morphologically diverse palaeotropical clade (*P.* sects. *Angostylidium* Müll.Arg. [P4] + *Hedraiostylus* (Hassk.) Müll.Arg. and *Madagascarienses* Card.-McTeag. & L.J.Gillespie [P5]). Cardinal-McTeague et al. (2019) estimated a mid-Oligocene origin for the genus in South America, with the split into the two main clades in the early Miocene. They hypothesized a single long distance dispersal event to Africa in the early Miocene, where the lineage diversified (*P.* sects. *Angostylidium* and *Hedraiostylus*), with subsequent single dispersals to Madagascar (*P.* sect. *Madagascarienses*) and southeastern Asia (*P. corniculata* Sm., *P.* sect. *Hedraiostylus*).

Plukenetia species are morphologically diverse and show considerable variation in staminate and pistillate flower morphology, and fruit and seed size and morphology (Gillespie 1993, 2007; Cardinal-McTeague et al. 2019; Cardinal-McTeague and Gillespie 2020). Cardinal-McTeague et al. (2019) studied seed size evolution in the genus and determined that seed size was positively correlated with plant size, fruit type and dispersal, and seedling ecology. Seeds vary from 4.5 to 56 mm long, 28 to 38,000 mm^3 in volume, and lenticular to ovoid or subglobose in shape (Cardinal-McTeague et al. 2019). Species in *P.* sections *Hedraiostylus* and *Penninerviae* are vines, slender lianas, or less often perennial herbs with small, dry capsules that explosively dehisce their small seeds. At the other extreme, *P. conophora* (monotypic *P.* sect. *Angostylidium*), *P. polyadenia* Müll.Arg., and *P. lehmanniana* (Pax & K.Hoffm.) Huft & L.J.Gillespie (*P.* sect. *Plukenetia*) are large, thick-trunked canopy lianas of wet forest with very large, fleshy indehiscent fruit and very large seeds. Among Old World taxa *P. conophora* is found in wet forest in central and west Africa, whereas species of *P.* sect. *Hedraiostylus* (4 spp.) are known from savanna and dry forest in southern and central Africa and moist to wet forest in southeastern

Asia (Gillespie 2007, 2023). *Plukenetia* section *Madagascarienses* (3 spp.), endemic to Madagascar and found in dry scrub or forest, has seed and fruit size and morphology intermediate between the two extremes, with seeds 13–18 mm long (850–2600 mm^3) and fruit large-sized and tardily dehiscent (Gillespie 2007; Cardinal-McTeague et al. 2019).

Over the last 15 yr the first author (LG) became aware of an unusual new species of *Plukenetia* from Madagascar, after receiving a gift for determination from MO (Thiers 2023). The collection (*Randrianaivo et al. 948*) was unusual for its elliptic, pinnately veined leaf blades, larger seeds, larger and apparently indehiscent fruit, and distribution on the wet east coast of Madagascar. Although lacking flowers, the collection was easily recognized as a species of *Plukenetia* by its 4-carpellate fruit, with one seed per locule, basilaminar nectaries, and liana habit. Until then, the genus was represented in Madagascar by three species of dry forest and scrub in the west, far north, and far south with ovate to suborbicular, palmately veined or 3-nerved leaf blades (Gillespie 2007). In the intervening years, two additional collections surfaced from eastern Madagascar. All three collections share pinnately veined leaves, a character previously thought to be exclusively found among neotropical species, specifically *P.* sects. *Penninerviae* and *Fragariopsis*.

A third new species from northeastern-most Madagascar was recently recognized among undetermined Euphorbiaceae specimens. Although vegetatively similar to other species of dry forest in Madagascar, the species is unusual for its flat androecium of sessile anthers on a flat receptacle, very different from the elongate androecia and receptacles of all other species in Madagascar.

Here we describe three new species of *Plukenetia* sect. *Madagascarienses* from eastern Madagascar. We present molecular, pollen, and floral morphological evidence to place the species in a phylogenetic context. In addition, we provide an emended description of *P.* sect. *Madagascarienses* and updated keys to the sections of *Plukenetia* and to the species of *P.* section *Madagascarienses*.

Materials and Methods

Specimens—Herbarium specimens of the new species were borrowed from MO, and additional specimens were examined at P and TAN. Herbarium acronyms follow Index Herbariorum (Thiers 2023). Online collection databases were searched extensively for additional specimens: Global Biodiversity Information Facility (GBIF), Tropicos, and online databases of K, G, and P herbaria. Searches were conducted for collections of *Plukenetia* not identified to species and those possibly misidentified from Madagascar. Fieldwork in Madagascar was undertaken during November to December 2012.

Morphology—Measurements were made on dried herbarium specimens, except for loose staminate flowers, which were rehydrated using a solution of water with a drop of liquid soap. Photographs of rehydrated staminate flowers and leaf, inflorescence, and flower details on herbarium specimens were taken with a Leica DVM6 microscope (Leica Microsystems, Wetzlar, Germany). Seed size categories and calculation of seed size volumes follow Cardinal-McTeague et al. (2019).

We examined pollen of two collections representing new species (*Antilahimena et al. 1803*, *Razafimandimbison et al. 416*); staminate flowers were not present on the other two collections. For comparison, we also examined pollen of two of the three known Malagasy species (*P. ankaranensis* and *P. madagascariensis*). Pollen grains were isolated and soaked in the same rehydrating solution, mounted on glass slides, and examined and measured using a compound light microscope. Dry pollen grains were mounted on stubs, sputter coated with a gold/palladium alloy, and examined on a FEI Apreo scanning electron microscope (SEM) (Thermo Fisher Scientific, Waltham, Massachusetts). Pollen quantity was insufficient for processing (e.g. acetolysis) to remove pollenkitt and other debris. Pollen terminology follows Erdtman (1966), Walker and Doyle (1975), and, specifically for tribe Plukenetieae, Gillespie (1994).

Molecular Phylogenetics—Four specimens, representing three new species, were extracted for sequencing: *Antilahimena et al. 1803* (CAN), *Randrianaivo et al. 948* (CAN), *Randrianasolo et al. 1598* (MO), and *Razafimandimbison et al. 416* (MO). Apart from these samples, the taxon set was derived from our previous phylogenies of *Plukenetia* (Cardinal-McTeague et al. 2019; Cardinal-McTeague and Gillespie 2020). We used a reduced taxon set that included all accessions of previously sampled palaeotropical species (6 spp.) and limited neotropical species to a maximum of two samples per species. Sequences were not available for two palaeotropical species belonging to sect. *Hedraiostylus*, each known only from their type collection (*P. kwangoensis*, *P. procumbens*). We included three samples of two closely related Plukenetieae subtribe Plukenetiinae genera, *Romanoa* Trevis. and *Haematostemon* Pax & K.Hoffm., as outgroups (Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019).

For genetic markers we chose the nuclear ribosomal external and internal transcribed spacers (ETS, ITS) consistent with our previous studies and based on their relatively high success rate for degraded samples and high sequence variation. Extraction, PCR amplification, and Sanger sequencing with BigDye^{TM} Terminator v3.1 chemistry on an ABI 3730xl DNA Analyzer (Thermo Fisher Scientific, Waltham, Massachusetts) largely followed Cardinal-McTeague et al. (2019). The extractions using modifications of the DNeasy Plant Mini Kit (Qiagen Inc., Valencia, California) protocol had careful contamination control measures with dedicated materials and equipment for degraded "antique DNA" and were not co-extracted with any other *Plukenetia* spp.

Sequence alignment, model selection, and Bayesian analysis follow methods outlined in Cardinal-McTeague et al. (2019), with the number of generations adjusted to 2 million. The optimal models of nucleotide evolution identified for each gene were GTR + I + G for ITS and HKY + I + G for ETS. Convergence metrics (i.e. standard deviation of split frequencies < 0.005, potential scale reduction factors near 1.0, effective sample sizes of each parameter > 200) were assessed as in Cardinal-McTeague et al. (2019). The alignment and MrBayes tree file are available on Dryad (Gillespie et al. 2024). Dataset characteristics, such as variable and parsimony informative characters, were calculated using the python package PhyKIT (Steenwyk et al. 2021).

Species Concept—We used a morphological species concept, relying on correlated morphological similarities among individuals to define species that are separated from each other by clear correlated morphological discontinuities ("morphological cluster" species concept sensu Knapp 2013; see also Mallet 1995; Knapp 2008). When only a single individual represents a putative species, then we relied only on multiple distinct morphological differences from other species. In defining species, we considered the level of variation found among species in *Plukenetia*, especially among putative sister species, with a focus on characters previously determined to be useful in the genus. Sequence data could not be used to assist in determining species boundaries, since insufficient data was obtained.

Distribution Map—The species distribution map was created in Google Earth Pro and edited in Adobe Illustrator. The mapping data are available on Dryad (Gillespie et al. 2024). The coordinates indicated on the label of *Razafimandimbison et al. 416* did not correspond to the locality given; the correct latitude is assumed to be 12°44′S, rather than 12°54′S (see Notes in Taxonomic Treatment).

Preliminary Conservation Assessments—Preliminary conservation assessments were made according to IUCN guidelines (IUCN 2012, 2022). Forest cover was estimated based on satellite photographs in Google Earth Pro. Since only one or two collections are known for each species and there is no information on population size or trends, we did not conduct analyses using software packages.

Results

Despite extensive online searches of herbarium collection databases, no additional collections of the new species were found, although additional specimens of several collections were located. In 2012 we searched for populations in the region of Manombe in southeastern Madagascar, both in the location where the original collection (*Randrianaivo et al. 948*) was made and in neighboring forest fragments of similar forest type and substrate. We also spent considerable time collecting in the Maroansetra area, although we did not attempt to revisit the original remote locality of the *Antilahimena et al. 1803* collection. No plants of *Plukenetia* were located in either area.

Morphology—Close examination of the three collections from wet forest in eastern Madagascar revealed that two distinct and disjunct species are represented, *P. randrianaivoi* sp. nov. from southeastern Madagascar, represented by two collections (*Randrianaivo et al. 948, Randrianasolo et al. 1598*) and *P. antilahimenae* sp. nov. from the region of Maroansetra in northeastern Madagascar (*Antilahimena et al. 1803*). Both species differ from all other *Plukenetia* species in Madagascar by their pinnately veined leaf blades, larger fruit, and larger seeds (20–30 mm long). Seeds were determined to be "extra-large" according to the seed size categories defined in Cardinal-McTeague et al. (2019): seed volumes are 3500–7500 mm^3 in *P. randrianaivoi* and ca. 6000 mm^3 in *P. antilahimenae*. These two new species, described below, may be distinguished most easily by indumentum type (pubescent vs. puberulent), distribution, and density, and geographical distribution. See Key and Taxonomic Treatment for details and additional distinguishing characters.

The collection *Razafimandimbison et al. 416* (MO) from Réserve Spéciale Analamerana on the eastern side of the northern tip of Madagascar represents a distinctive third new species, *P. analameranensis* sp. nov., distinguished from all other Malagasy species by its flat androecium, and from the above two new species by its palmately veined leaves. No fruit or seeds were present on this collection.

Pollen SEM images are presented in Fig. 1. All four species examined have tricolpate pollen but differ in tectum morphology. Of the two new species sampled, *P. antilahimenae* has a reticulate tectum (Fig. 1A–C) and *P. analameranensis* a finely reticulate tectum (Fig. 1D, E), both with relatively broad muri and small lumina and with muri crenate (transversely ridged) to scabrate. Based on these results we decided to re-examine pollen of two known species from Madagascar (described previously in Gillespie 1994, 2007). *Plukenetia madagascariensis* was found to have a distinctly foveolate tectum (Fig. 1H, I) with a smooth surface between pits, whereas *P. ankaranensis* has a tectum that appears mostly rugulate (i.e. with irregularly distributed, curved or wavy, elongate sculpture elements separated by grooves and pits) with a microverrucate surface (Fig. 1F, G). In the latter species the tectum may approach foveolate near the colpi or sometimes reticulate (with very broad muri). Pollen of the two new species is described in detail in the Taxonomic Treatment section.

Molecular Phylogeny—Amplification and sequencing of only one of four collections was successful (Appendix 1); all four collections were preserved in alcohol in the field prior to drying resulting in poor quality leaf material with highly degraded DNA. ETS and ITS sequences were obtained for one collection of *P. randrianaivoi*, *Randrianasolo et al. 1598* (CAN).

The combined ETS+ITS dataset comprised 45 samples and had a total aligned length of 1270 characters (ETS: 469, ITS: 801) with 536 variable characters (ETS: 239, ITS: 297), and of these 460 are parsimony informative (ETS: 199 [42.4%], ITS: 261 [32.6%]). The combined ETS+ITS Bayesian consensus tree with posterior probability (PP) values is shown in Fig. 2. Strong branch support, interpreted as PP ≥ 0.95, is indicated by bold branches.

Plukenetia randrianaivoi was recovered in the sect. *Madagascarienses* clade (PP = 1), within subclade P5 (PP = 1) of the palaeotropical clade (PP = 0.97), all three nested clades strongly supported. The palaeotropical and sect. *Plukenetia* clades comprise the strongly supported palmately veined major clade (PP = 1), sister to the pinnately veined clade (PP = 1). Within sect. *Madagascarienses P. randrianaivoi* was sister to *P. ankaranensis* (PP = 1), and these sister to a clade of *P. decidua* and *P. madagascariensis* (PP = 0.95).

Discussion

Previous phylogenetic analyses showed that palaeotropical species of *Plukenetia* are strongly supported as monophyletic despite their very different morphologies (Cardinal-McTeague et al. 2019; Cardinal-McTeague and Gillespie 2020). Cardinal-McTeague et al. (2019) provided evidence for the shared morphologies of *P.* sect. *Angostylidium* and some species in the neotropical *P.* sect. *Plukenetia* (e.g. very large fruit and seeds, presence of interstaminal nectaries) as plesiomorphic in the palmately veined major clade. They also suggested that the morphologies of *P.* sects. *Hedraiostylus* and *Madagascarienses* are derived (e.g. shared absence of floral nectaries). Although *P.* section *Hedraiostylus* shares similar small dry capsules and small seeds with the neotropical *P.* section *Penninerviae*, these features appear to be independently derived.

The three new species of *Plukenetia* described here are unique among palaeotropical species, *P. randrianaivoi* and *P. antilahimenae* in their elliptic, pinnately veined leaf blades and *P. analameranensis* in its androecium of sessile anthers on a broad flat receptacle (also unique in the genus). Despite their divergent morphologies these new species from Madagascar are clearly members of *P.* sect. *Madagascarienses*. Although only one species (*P. randrianaivoi*) was successfully sequenced and determined to be firmly embedded in the *P.* sect. *Madagascarienses* clade (Fig. 2), the character combination of sessile anthers, absence of nectaries, and large fruit and seeds support placement of the other two new species here. In addition, *P. antilahimenae* is morphologically very similar to *P. randrianaivoi* and has elongate staminate receptacles and androecia characteristic of *P.* sect. *Madagascarienses* members (Fig. 3C, D), contrasting with androecia of anthers sessile or on filaments on flat, convex, or subglobose receptacles in all other sections (Gillespie 1993, 2007). Apart from its unusual androecium *P. analameranensis* closely resembles *P. ankaranensis*, sharing very similar pistillate flower and leaf morphology (Fig. 3; Gillespie 2007: figure 2). These three new species greatly expand the morphological diversity of the section and the palaeotropical clade and provide yet more examples of convergence and independent origin of morphological characters in the palaeotropical clade.

Species Relationships and Diversification in Madagascar—Based on the phylogenetic tree, the four Malagasy species sampled resolved as two subclades, with *P. randrianaivoi* sister to *P. ankaranensis*, and *P. decidua* and *P. madagascariensis* as sister species. We were initially surprised about the close relationship of *P. randrianaivoi* with *P. ankaranensis* given the very different leaf architecture and larger fruit and seeds of *P. randrianaivoi* compared to the other species. However, further study revealed a set of characters shared among the three new species and *P. ankaranensis.* They share fully connate styles that are obovoid, obconical, or otherwise massive (Figs. 3A, 4C, 5B, C) (unknown in *P. antilahimenae*) and pollen

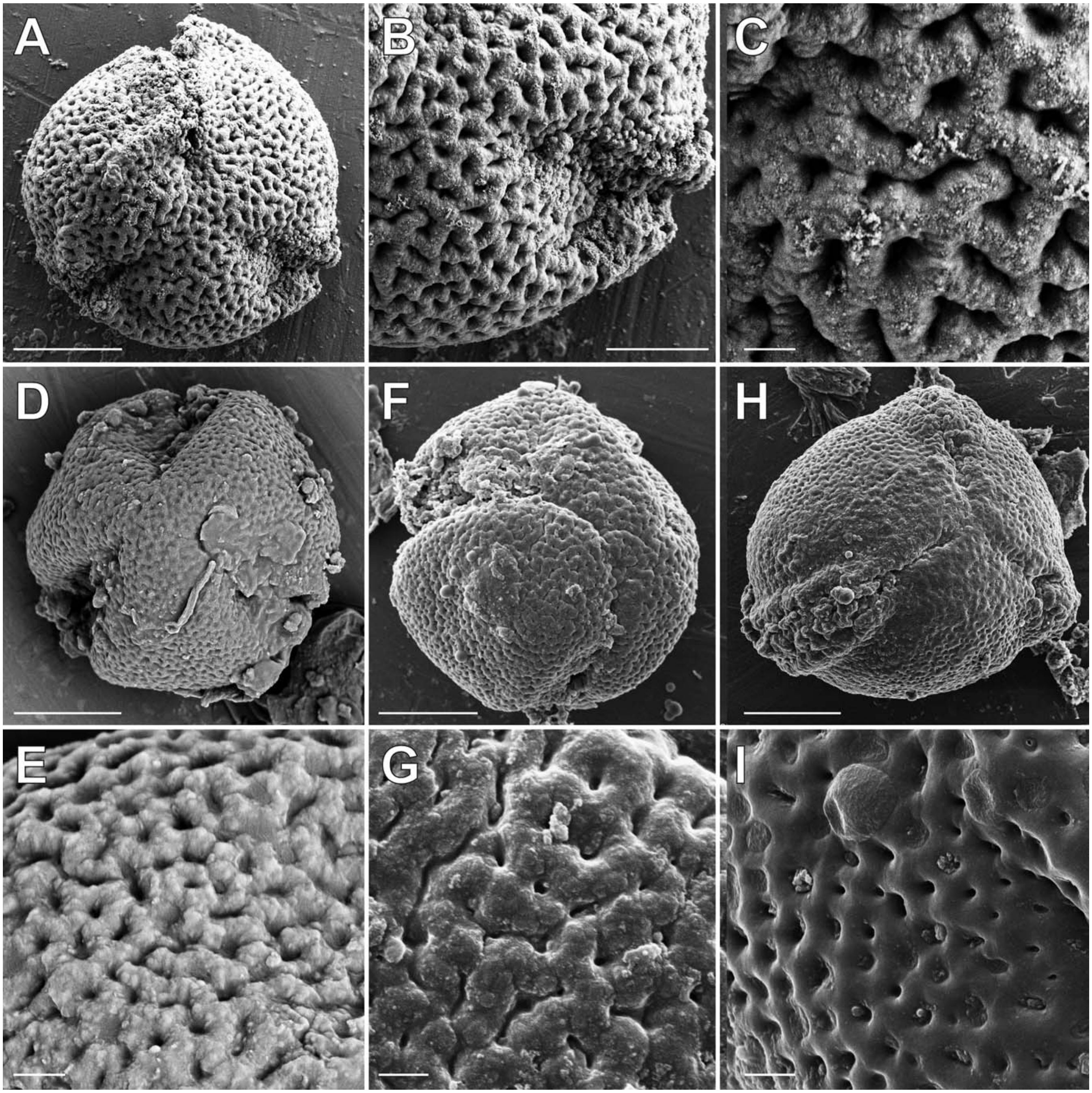


FIG. 1. Scanning electron micrographs of pollen of *Plukenetia* sect. *Madagscarienses*. A–C. *P. antilahimenae* (*Antilahimena et al. 1803*). D–E. *P. analameranensis* (*Razafimandimbison et al. 416*). F–G. *P. ankaranensis* (*Gillespie 4074*). H–I. *P. madagascariensis* (*Andrianjafy et al. 1648*). A, D, F, H. Pollen grain. B. Closeup of colpus. C, E, G, I. Closeup of exine. Images by P. Sokoloff and L. Gillespie. Scale bars: A, D, F, H = 10 μm; B = 5 μm; C, E, G, I = 1 μm.

exines that are reticulate or rugulate (Fig. 1A–G) (unknown in *P. randrianaivoi*) in contrast to the cylindrical, partly connate styles and distinctly foveolate pollen of *P. decidua* and *P. madagascariensis* (Figs. 1H, I, 3B; Gillespie 2007). Additional shared characters include shorter styles (1.8–5.5 mm long) and smaller staminate flowers (unknown in *P. randrianaivoi*) with shorter sepals (1.2–2.2 mm long) and shorter androecia (to 1 mm long) with mostly fewer anthers (15–24) (Figs. 3A, C, 4C, D, 6F), compared to longer styles (8–22 mm) and larger staminate flowers (sepals 3–6 mm, androecia 1.6–4 mm, 18–60 + anthers) of *P. decidua* and *P. madagascariensis* (Fig. 3B, D; Gillespie 2007). We suggest that *P. analameranensis*, *P. ankaranensis*, *P. antilahimenae*, and *P. randrianaivoi* form a subclade sister to *P. decidua* and *P. madagascariensis*.

Plukenetia underwent a species radiation in Madagascar, compared to other palaeotropical areas. *Plukenetia* sect. *Madagascarienses* was estimated to have diverged from its sister *P.* sect. *Hedraiostylus* in the late Miocene (stem age 9.41 Mya) and radiated in the late Miocene (crown age 7.1 Mya) (Cardinal-McTeague et al. 2019). This species radiation resulted in the evolution of diverse morphologies including the unique androecium of sessile anthers on a flat receptacle

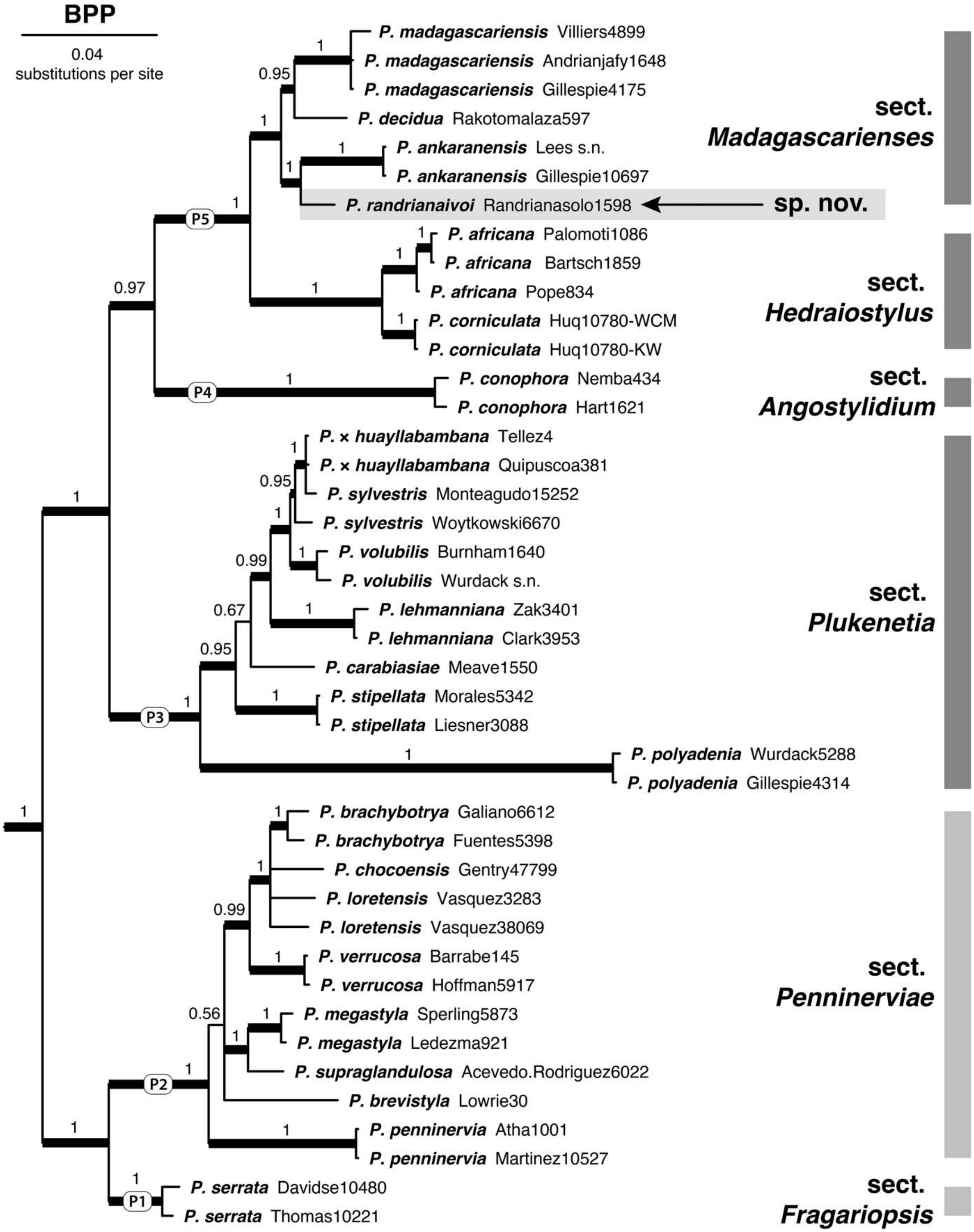


FIG. 2. Bayesian 50% majority rule consensus tree based on a 47 accession ETS+ITS dataset for *Plukenetia* and Plukenetiinae outgroups (latter not shown). Bayesian posterior probability (PP) support values > 0.50 are indicated on each branch; branches in bold indicate strong support, PP ≥ 0.95). Subclades P1–P5 were defined in Cardinal-McTeague and Gillespie (2016); sections in the pinnately veined clade (P1 + P2) are indicated by light grey boxes, those in the palmately veined clade (P3–P5) by dark grey boxes.

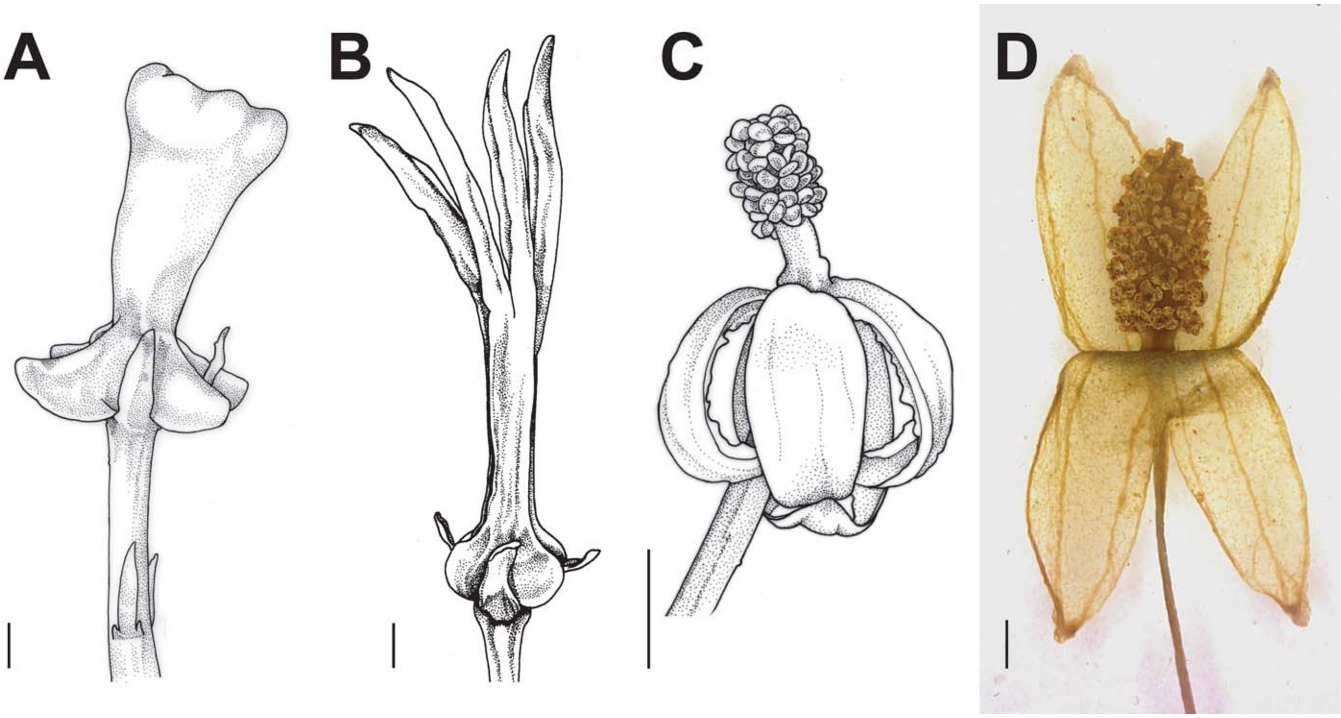


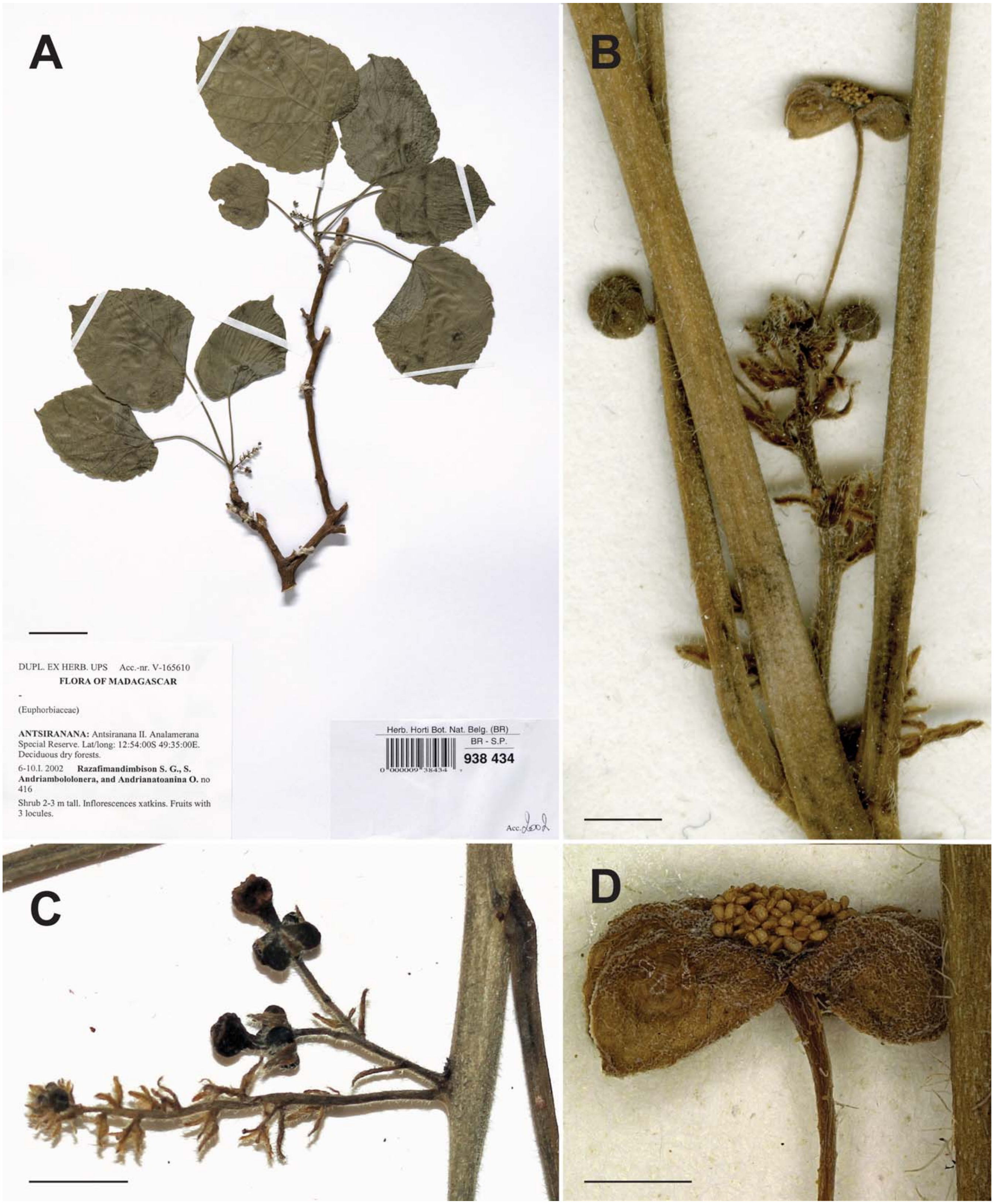
FIG. 3. Flowers of *Plukenetia* sect. *Madagascarienses* species. A. *P. ankaranensis*, pistillate flower (*Gillespie 4074*). B. *P. decidua*, pistillate flower (*Capuron SF 27952*). C. *P. ankaranensis*, staminate flower (*Gillespie 4074*). D. *P. madagascariensis*, staminate flower (*Andrianjafy et al. 1648*). A–C illustrations by Susan Laurie-Bourque reproduced from Gillespie (2007) with permission from *Systematic Botany*; D image by P. Sokoloff and L. Gillespie. Scale bars = 1 mm.

of *P. analameranensis* (Fig. 4D). Of note is the independent evolution of several leaf and pollen characters, specifically pinnately veined leaf blades (Figs. 5A, 6A) and reticulate pollen (Fig. 1A–C) that look remarkably similar to the leaves and pollen of the neotropical *P.* sects. *Penninerviae* and *Fragariopsis* (Gillespie 1993: figures 2, 10, Gillespie 1994: figures 20–24, 28–29). These newly described diverse morphologies within *P.* sect. Madagascarienses blur the morphological boundary between the two major clades of *Plukenetia* (Cardinal-McTeague et al. 2019).

Plukenetia Major Clades Lack Defining Morphological Characters—Two major clades of *Plukenetia* are strongly supported in molecular analyses and were thought to be morphologically coherent (Cardinal-McTeague and Gillespie 2016, 2020; Cardinal-McTeague et al. 2019). The neotropical pinnately veined clade (*P.* sects. *Penninerviae* and *Fragariopsis*) was characterized by elliptic, acute-based, pinnately veined leaf blades and reticulate pollen, and the pantropical palmately veined clade (*P.* sects. *Angostylidium*, *Hedraiostylus*, *Madagascarienses*, and *Plukenetia*) by exclusively ovate, round- to cordate-based, palmately veined leaf blades with 3–7 primary veins and foveolate pollen.

The morphological characterization of these two clades based on leaf venation and shape, two partly correlated characters, still holds for most species; however, there are now multiple exceptions. The neotropical species *P. verrucosa*, with leaf blades ovate with subcordate to truncate bases and palmate venation with three primary veins, has long been known as an exception in the pinnately veined clade and an unusual member of *P.* sect. *Penninerviae* (Gillespie 1993; Gillespie and Armbruster 1997: figure 12; Cardinal-McTeague and Gillespie 2020). Cardinal-McTeague et al. (2019) showed that *P. verrucosa* is nested within the pinnately veined clade and these features derived independently from the palmately veined clade. The recently described *P. kwangoensis* (Gillespie 2023) is an exception in the palmately veined clade; its linear-oblong leaf blades with narrowly acute bases are pinnately veined with a single primary vein, although sometimes a faint lateral basal vein pair is present. In *P. africana*, which has extremely variable shaped leaf blades often with hastate bases and usually palmate venation, only a single primary vein is typically present on linear non-hastate blades (Gillespie 2023). In *P.* section *Hedraiostylus*, where these two species belong, primary venation pattern appears to be correlated with leaf blade width with a trend towards loss of lateral primary veins as leaf blades become narrower. Here we add two more exceptions to the palmately veined clade, *P. antilahimenae and P. randrianaivoi*, which have elliptic pinnately veined leaf blades that are very similar to and virtually indistinguishable from those of the pinnately veined clade.

Pollen exine morphology has also been used to characterize the two major clades of *Plukenetia*, with all species in the palmately veined clade having pollen with a foveolate tectum and those in the pinnately veined clade having exclusively reticulate pollen (Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019). Upon examining two of the three new Malagasy species, we were surprised to discover that they did not have foveolate pollen as expected; *P. antilahimenae* has pollen with a coarsely reticulate tectum (Fig. 1A–C), remarkably similar to pollen of *P.* sects. *Penninerviae* and *Fragariopsis* species (Gillespie 1994: figures 20–24, 28–29 [as *Vigia*]) and *P. analameranensis* has pollen with a finely reticulate tectum (Fig. 1D, E). Based on these results we re-examined two previously known *P.* sect. *Madagascarienses* species and confirmed that *P. madagascariensis* has foveolate pollen (first described in Gillespie 1994) (Fig. 1H, I). The



DUPL. EX HERB. UPS Acc.-nr. V-165610
FLORA OF MADAGASCAR
-
(Euphorbiaceae)

ANTSIRANANA: Antsiranana II. Analamerana Special Reserve. Lat/long: 12:54:00S 49:35:00E. Deciduous dry forests.

6-10.I. 2002 **Razafimandimbison S. G., S. Andriambololonera, and Andrianatoanina O.** no 416

Shrub 2-3 m tall. Inflorescences xatkins. Fruits with 3 locules.

FIG. 4. *Plukenetia analameranensis* sp. nov., *S. G. Razafimandimbison et al. 416.* A. Holotype specimen (BR 938434). B. Inflorescence with open staminate flower and buds (MO). C. Inflorescence with two pistillate flowers (UPS). D. Staminate flower (MO). A image copyright Meise Botanic Garden, used with permission; B, D by P. Sokoloff; C by M. Hjertson. Scale bars: A = 3 cm; B = 2 mm; C = 5 mm; D = 1 mm.

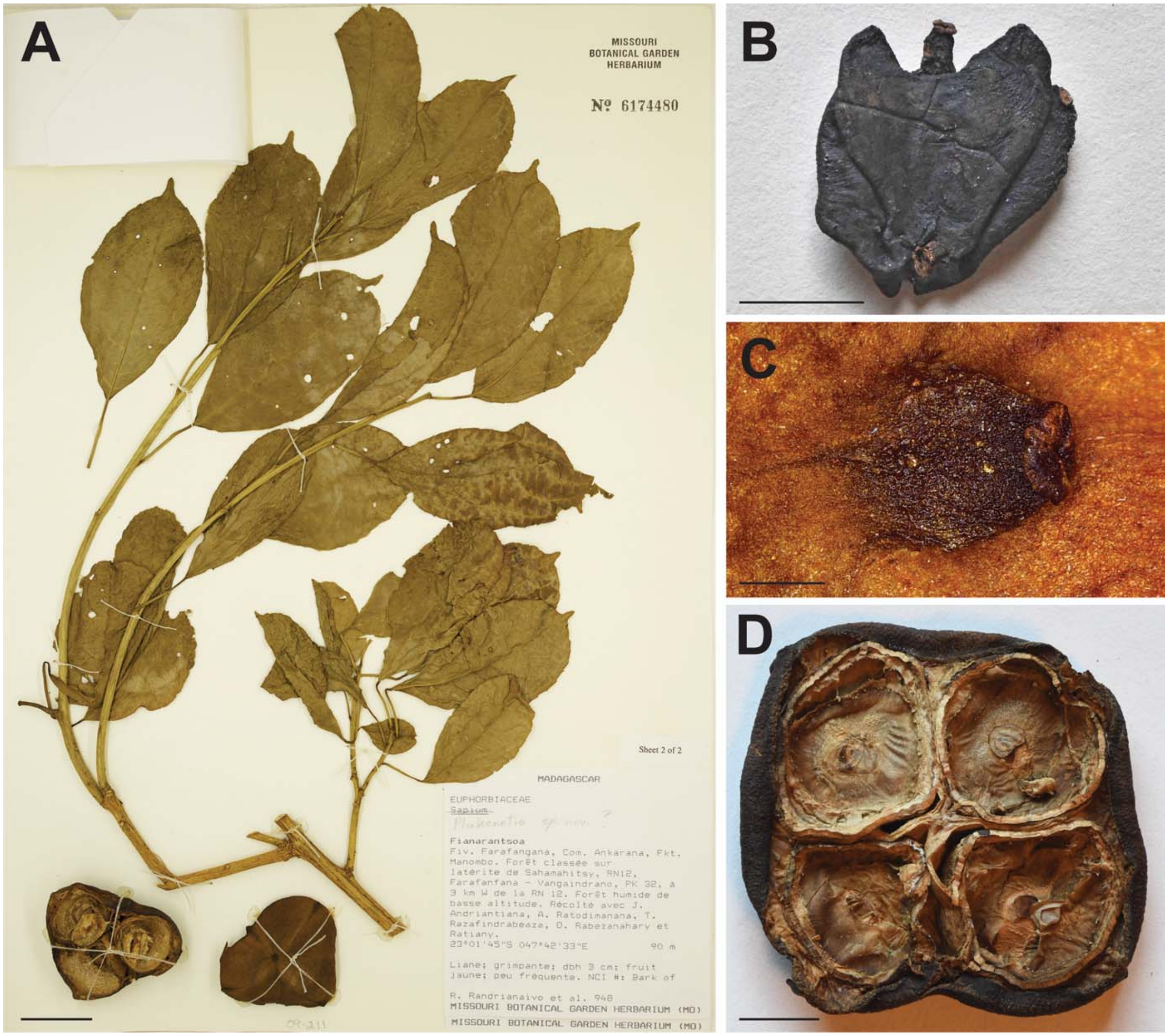


FIG. 5. *Plukenetia randrianaivoi* sp. nov., *R. Randrianaivo* et *al. 948*. A. Holotype specimen (MO 6174480, sheet 2/2), fruit with only 3 of 4 carpels developed. B. Immature fruit (CAN). C. Style column on mature fruit (MO, sheet 2). D. Fruit cross-section (CAN). A image by L. Sharpe; B–D by P. Sokoloff. Scale bars: A = 3 cm; B = 5 mm; C = 1 mm; E = 1 cm.

second species, *P. ankaranensis*, previously described as having foveolate pollen based on LM (Gillespie 2007), was found to have pollen with a mostly rugulate tectum, which may possibly represent a stage intermediate between foveolate and reticulate (Fig. 1F, G). *Plukenetia* section *Madagascarienses* is the only section of *Plukenetia* to show this level of variation in tectum morphology. Elsewhere in tribe Plukenetieae, pollen morphology is an important and conservative taxonomic character that characterizes genera or, in the case of the large genus *Tragia*, sections (Gillespie 1994; Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019).

Both pinnately veined, elliptic leaf blades and reticulate pollen appear to be derived features that evolved in parallel independently in the pinnately veined clade and within *P.* sect. *Madagascarienses* and provide good examples of convergent evolution. The alternative scenario of these character states as plesiomorphic and palmately veined, ovate leaf blades and foveolate pollen as derived, with reversals in *P. antilahimenae*, *P. randrianaivoi* (pollen unknown), and *P. analameranensis* (pollen only), is less likely given that the sister to *Plukenetia*, *Romanoa*, has triangular to ovate, palmately veined leaf blades and finely foveolate-fossulate pollen. Given that the two new species with pinnately veined, elliptic leaf blades (and reticulate pollen) inhabit wet forest (all other Malagasy species occupy dry or semi-dry forest) as do most species in the pinnately veined clade, are these characters somehow functionally correlated with wet forest habitat and/or a wetter climate? Among the many determinants of leaf shape, plant-water relations are thought to be among the most important (Nicotra et al. 2011). Lobed leaf blades with a greater number of large veins for more efficient water conduction are thought to be adaptive in drier climates, whereas elliptic leaves may be more adaptive in wetter climates (e.g. better at shedding water). A possible relationship

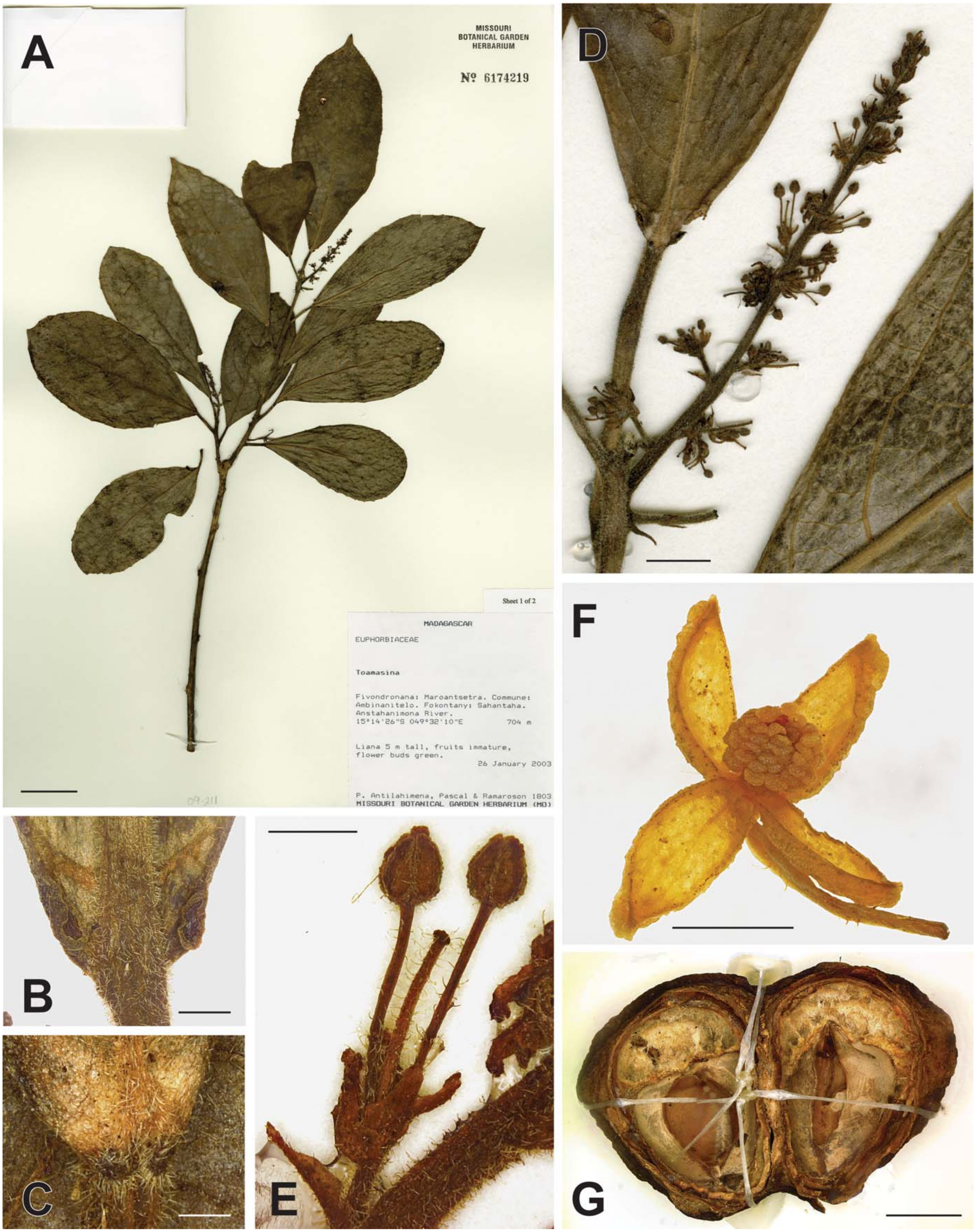


FIG. 6. *Plukenetia antilahimenae* sp. nov., *P. Antilahimena et al. 1803*. A. Holotype specimen (MO 6174219, sheet 1/2). B. Leaf abaxial surface showing adaxial basilaminar nectaries on revolute margin. C. Leaf adaxial surface showing knob-like stipels. D. Inflorescence. E. Cyme of staminate flower buds. F. Staminate flower (rehydrated mature bud with sepals pulled apart, several anthers missing from apex of androecium) (CAN). G. Fruit, longitudinal cross-section (MO 6174220, holotype sheet 2). A–E, G images by P. Sokoloff; F by P. Sokoloff and L. Gillespie. Scale bars: A = 3 cm; B, C, E, F = 1 mm; D = 5 mm, G = 1 cm.

between wet versus dry climate and pollen tectum morphology is more difficult to explain but may be related to harmomegathy, the ability of pollen to withstand expansion-contraction stresses, such as those that occur during desiccation, or to reproductive biology (cavity size affects quantity of material functioning in adhesion and/or recognition that can be held on the pollen surface) (Muller 1979; Volkova et al. 2013; Wang and Dobritsa 2018).

We are not aware of any characters that now exclusively define the two major clades of *Plukenetia*. As noted above, venation pattern and pollen tectum morphology work for the majority of species, but there are now multiple exceptions. Style connation and geography are other characters that can be used to assign species to one of the two major clades, but again there are exceptions. Species of the neotropical pinnately veined clade have short styles that are fully connate (Gillespie 1993; Cardinal-McTeague and Gillespie 2020). Species of the palmately veined clade are neotropical or paleotropical and have short to long styles that are partly connate, except for four palaeotropical species, *P. analameranensis, P. ankaranensis, P. corniculata*, and *P. randrianaivoi* (pistillate flowers unknown in *P. antilahimenae*) with short fully connate styles (Figs. 1A, 4C, 5B, C) (Gillespie 2007; Cardinal-McTeague and Gillespie 2020).

More collections, especially those with pistillate flowers (*P. antilahimenae*, *P. randrianaivoi*), staminate flowers (*P. randrianaivoi*), and fruit (*P. analameranensis*), plus additional molecular data, are needed to more completely describe and understand these three new species. Including these species in *P.* section *Madagascarienses* necessitates emending the sectional description and revising the key to sections (first published in Cardinal-McTeague and Gillespie 2020).

Taxonomic Treatment

Plukenetia sect. *Madagascarienses* Card.-McTeag. & L.J.Gillespie, Syst. Bot. 45: 518. 2020. Type: *Plukenetia madagascariensis* Leandri.

Emended description [derived from Cardinal-McTeague and Gillespie (2020)]:

Lianas, stems slender to thick. Leaf venation palmate or pinnate, primary veins 1 or 3(–5). Inflorescences bisexual racemes or racemose thyrses; pistillate flowers solitary at 1–2 basal-most nodes or 1–2 in basal cymule; staminate flowers 1/node or in condensed or lax 1–7-flowered cymules. Staminate flowers: receptacle usually enlarged and ellipsoid, oblong-cylindrical, or ovoid-conical (flat in *P. analameranensis*); nectaries absent; stamens 15–60+, densely or loosely packed; filaments absent; pollen $p = 28–41\ \mu m$, $E = 35–51\ \mu m$, tectum foveolate, reticulate, or rugulate. Pistillate flowers: styles entirely connate into an obconic, obovoid, or cylindric column, 2.5–5.5 mm long, or 50–70% connate, 8–16 mm long, column cylindrical, free style arms slender and tapered. Fruits 4-lobed, tardily dehiscent capsules or apparently indehiscent, 2.3–6 cm in diam. Seeds broadly ellipsoid or subglobose, 13–30 × 11–24 × 11–24 mm ("large" or "extra-large" sensu Cardinal-McTeague et al. 2019).

Species—6 spp.: *P. analameranensis*, *P. ankaranensis*, *P. antilahimenae*, *P. decidua*, *P. madagascariensis*, *P. randrianaivoi*.

Key to the Sections of *Plukenetia*

[Modified from Cardinal-McTeague and Gillespie (2020)]

1. Fruits 0.9–2 cm in diam, dry capsules; styles 0.3–4.5 mm long 2
    2. Anthers on short filaments; pollen tectum foveolate; Africa, Southeast Asia .... *P.* sect. *Hedraiostylus*
    2. All or most anthers sessile; pollen tectum reticulate; Neotropics .... *P.* sect. *Penninerviae*
1. Fruits 2.3–11 cm in diam, dry to fleshy, capsules or indehiscent; styles 2.5–35 mm long 3
    3. Anthers sessile; nectaries absent in staminate flowers
        4. Staminate receptacles cylindrical, narrowly conical, ellipsoid, oblong-ellipsoid, or flat, not visible or partly visible between anthers; pistillate flowers (0) 1–2 (3) per inflorescence; Madagascar .... *P.* sect. *Madagascarienses*
        4. Staminate receptacles globose, clearly visible between scattered anthers; pistillate flowers 1–10 per inflorescence; Atlantic Forest region of Brazil .... *P.* sect. *Fragariopsis*
    3. Anthers on short-conical or slender-cylindrical filaments, 0.5–3 mm long; nectaries present on staminate flowers, interstaminal, slender-cylindrical, ligulate, or small to large and irregularly shaped (absent in *P. volubilis*) 5
        5. Stylar columns funnel-shaped, free style arms conspicuously dilated and spreading; stipels and glandular knobs absent at petiole apex; tropical central and western Africa .... *P.* sect. *Angostylidium*
        5. Stylar columns cylindrical, free style arms more or less uniform in thickness or tapered and erect or spreading; stipels or glandular knobs present adaxially at petiole apex; Neotropics .... *P.* sect. *Plukenetia*

Plukenetia analameranensis L.J.Gillespie, sp. nov. Type: Madagascar. Antsiranana, [Diana Region], Analamerana Special Reserve, 12°54′S, 49°35′E [−12.9°S 49.58°] (corrected to 12°44′S, 49°35′E [−12.73°, 49.58°]), 6–10 Jan 2002, *S. G. Razafimandimbison, S. Andriambololonera & O. Andrianatoanina 416* (holotype: BR [photo!] [00000938434]; isotypes: K!, MO! [6463202], TAN, UPS [photo!] [V-165610]).

Plukenetia analameranensis differs from all other species of *P.* sect. *Madagascarienses* by its staminate flowers with a flat, broad receptacle and androecium (versus cylindrical, narrowly conical, or ellipsoid). It differs from *P. ankaranensis,* with which it is most similar, by its hirsute indumentum (hairs 0.4–0.6 mm long), shorter inflorescences (0.8–2 cm long), subglobose or suboblate staminate buds with a rounded apex, and a 4-winged ovary with rounded wings [versus finely puberulous indumentum (hairs ca. 0.1 mm long), inflorescences (2–)5–16 cm long, ovoid buds with a bluntly acute apex, and a 4-horned ovary with conical horns]. It differs from *P. madagascariensis* and *P. decidua* by its styles completely connate into an obovoid stylar column (versus partly connate and cylindrical), and from *P. antilahimenae* and *P. randrianaivoi* in its broadly ovate leaf blades with shallowly cordate bases and venation 3-nerved at base or weakly palmate (versus elliptic or obovate-elliptic leaf blades with acute or obtuse bases and venation pinnate with a single primary vein).

Monoecious woody plant; stems sparsely hirsute (hairs 0.4–0.6 mm long), older branches thick, woody, yellow-brown, glabrescent, leafy stems 1.2–2.5 mm diam. **Leaves** alternate, simple; stipules thick, ovate to triangular, minute, 0.3–0.5 mm long; petiole 3–12 cm long, moderately hirsute; blade broadly ovate, 5–10 × 4–8 cm, L/W = 1.0–1.3, chartaceous, both surfaces glabrate to sparsely hirsute with major veins sparsely to moderately hirsute, base shallowly cordate, often asymmetrical, with sinus 0.1–1.0 mm deep, margins crenate-serrate, teeth glandular, apex short-acuminate with tip 0.3–0.7 mm long, venation 3-nerved at base or weakly palmate, secondary veins 2–3 on each side of midrib, semicraspedodromous, tertiary veins percurrent or sometimes reticulate; stipels or glandular knob absent at petiole apex; adaxial basilaminar nectaries 2, elliptic, 0.2–0.4 mm long, marginal, 0.5–1.5 mm from blade base; abaxial laminar glands absent. **Inflorescences** bisexual or sometimes staminate, terminal (becoming leaf-opposed), racemose thryses, 0.8–2 cm long, axes hirsute; peduncle 0–2.5 mm long; pistillate flowers 1–2 on basal-most cymule, sometimes cymule bisexual with one or more staminate flowers, primary cyme axis 2–6 mm long; staminate flowers numerous above in cymules, cymules condensed, 1–2-flowered, primary cyme axes 0.5–3 mm long; bracts linear-lanceolate, hirsute, eglandular, staminate 1.5–2.5 mm long, pistillate 2.5–4 mm long; staminate bracteoles 0.5–1.5 mm long, pistillate to 2 mm long. **Staminate flowers:** pedicels jointed, 3.5–5 mm long, sparsely hirsute, persistent part 0.5–1 mm long; bud subglobose or suboblate, rounded at apex; sepals 4, broadly ovate, 1.3–1.8 × 1.3–1.8 mm (L/W = 1–1.2), sparsely hirsute, broadly acute to obtuse at apex, open wide and somewhat recurved at anthesis; androecium flat, 2.2 mm across, comprising ca. 18–24 sessile anthers densely packed on a broad flat receptacle; nectary absent. **Pistillate flowers:** pedicel 1.5–4 mm long, sparsely hirsute; sepals triangular-lanceolate, 1.8–2.2 × 0.8–0.9 mm, sparsely hirsute, often moderately hirsute near base and near margin distally; ovary 4-locular, 1.2–2 × 2.5–4 mm (including wings), 1 ovule/locule, hirsute, 4-winged, wings rounded, laterally compressed, sparsely hirsute to glabrate; styles completely connate into an obovoid column, 1.8–3 mm long, 0.5–1 mm wide at base, dilated to 1.6–2.4 mm distally, sparsely hirsute to glabrate, stigmas forming a lobed circular disc at apex. **Fruits** and **seeds** not seen. Figure 4.

Pollen—Tricolpate, suboblate (P/E = 0.75–0.80), polar axis ca. 22–30 µm, equatorial axis 30–38 µm; amb subcircular; colpus with margins uneven, exine semitectate-finely reticulate, often fragmented and/or gemmate at the colpus margin, muri scabrate to crenate (transversely ridged), lumina small, often narrower than muri (voucher: *Razafimandimbison et al. 416*, MO). Figure 1D, E.

Distribution and Habitat—This species is known only from Réserve Spéciale Analamerana in northernmost Madagascar where it grows in deciduous dry forest (Fig. 7). Most of the reserve is on a Mesozoic limestone plateau dissected by faults (Du Puy and Moat 1996; Goodman et al. 2018). The single flowering collection was made in January.

Etymology—The specific epithet refers to Réserve Spéciale Analamerana, the only place the species is known from.

Notes—Staminate flowers having a broad flat receptacle densely covered in small sessile anthers is a unique feature of this species (Fig. 4D), very different from the elongate androecia and receptacles of all other Madagascar species (unknown in *P. randrianaivoi*) (Fig. 3C, D). This species is morphologically most similar to *P. ankaranensis*, which is restricted to the Ankarana karst massif in Réserve Spéciale Ankarana, located only about 20 km west of Réserve Spéciale Analamerana. The two species share a similar completely connate, obovoid stylar column (Figs. 3A, 4C).

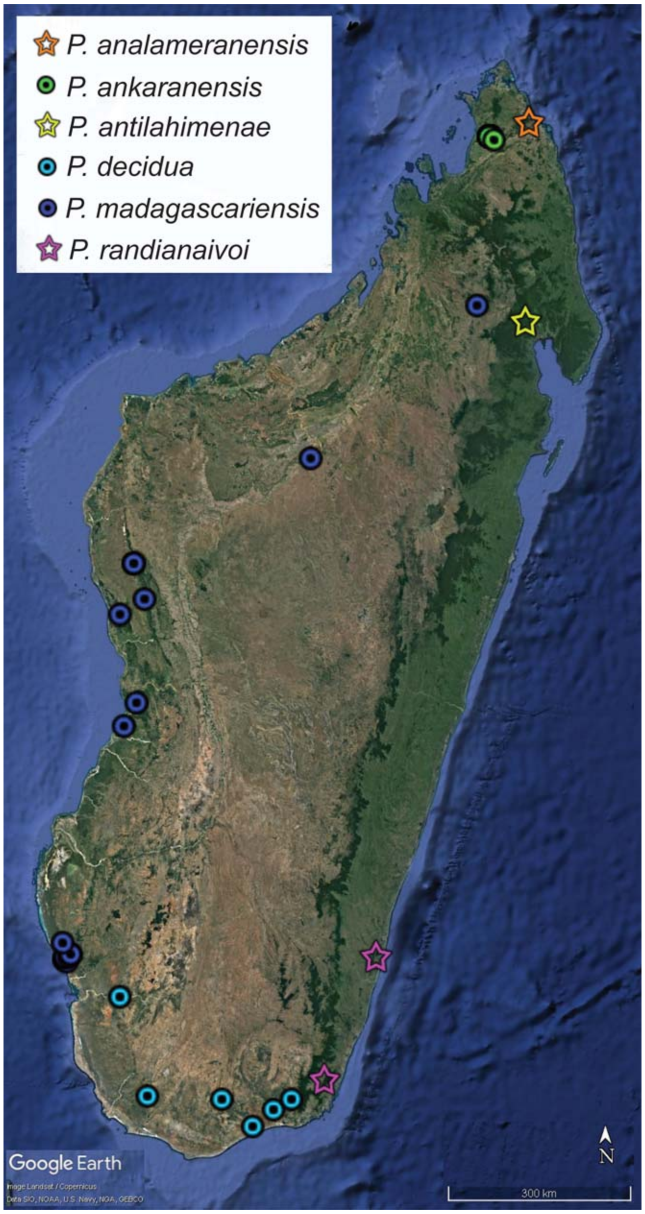


Fig. 7. Distribution map of species in *Plukenetia* sect. *Madagascarienses*. New species, *P. analameranensis*, *P. antilahimenae*, and *P. randrianaivoi*, shown by stars, previously described species by circles.

The specimen at BR is designated as holotype since it is the only specimen with both staminate flowers and intact pistillate flowers (Fig. 4A). The label of the type collection indicates that the collection was made in Réserve Spéciale Analamerana (entirely within the Diana Region and north of the Irodo River) in deciduous dry forest. However, the latitude-longitude given on the label indicates a locality south of the Irodo River in the Sava Region, which based on Google Earth Pro images is on a dry open plain with very sparse scattered shrubs and/or trees. We suggest that the latitude was incorrectly recorded; a latitude of 12°44′S, rather than 12°54′S, would place the locality in forest in the southeastern part of the reserve at an elevation of about 250 m (as mapped in Fig. 7).

Although the herbarium label indicates a shrub 2–3 m tall, this may not be accurate. The species is most likely a liana or scandent shrub since all other Malagasy species are lianas and the majority of species in the genus are lianas or vines (exceptions are two poorly known African species of *P.* sect. *Hedraiostylus*, which are assumed to be perennial herbs with woody rootstocks). Although recorded as in both flower and fruit, no fruits or seeds were seen, nor is there evidence on the specimens of fruiting pedicels; the collectors may have mistaken the female flowers for fruit.

Conservation Status—*Plukenetia analameranensis* is known from a single collection from Réserve Spéciale Analamerana. Potential threats include forest degradation or loss from wood and forest product exploitation and fire, specifically grassland fires extending into the forest edge (Goodman et al. 2018). In recent years deforestation in this large park (347 km^2) has been minimal overall (0.7% forest loss between 1996 and 2016) and is not occurring or very minimal in the eastern sector where the single collection is thought to be from (Goodman et al. 2018).

Given the uncertainty regarding the location of this collection (coordinates conflict with presence in Réserve Spéciale Analamerana), and thus the difficulty in assessing threats, we recommend a provisional IUCN status of Data Deficient. The species could be assessed as either Critically Endangered (B1B2abiii) or Least Concern depending on where it occurs in the reserve (assuming it does occur in the reserve) and the corresponding level of threat. If our hypothesis on the actual coordinates of the single collection locality is correct, then a provisional IUCN status of Least Concern may be most appropriate given that threats are minimal or non-existent across the eastern sector of the reserve, including the area of the assumed collection site.

Plukenetia antilahimenae L.J.Gillespie, sp. nov. TYPE: MADAGASCAR. Toamasina, [Analanjirofo region], Fivondronana Maroansetra, Commune Ambinanetelo, Fokontany Sahantaha, [Parc Naturel de Makira], Anstahanimona River, 704 m, 15°14′26″S, 49°32′10″E [−15.241°, 49.536°], 26 Jan 2003, *P. Antilahimena, O. Pascal & Ramaroson 1803* (holotype: MO, 2 sheets! [6174219, 6174220], isotypes: CAN!, TAN).

Plukenetia antilahimenae differs from *P. randrianaivoi* in its stems and inflorescence axes pubescent, petioles pubescent throughout, leaf blade abaxial surfaces sparsely pubescent with veins pubescent, and larger stipules (0.7–1.2 mm long). It differs from *P. analameranensis, P. ankaranensis*, *P. decidua*, and *P. madagascariensis* in its elliptic or obovate-elliptic leaf blades with acute or obtuse bases and venation pinnate with a single primary vein (versus leaf blades ovate, oblong-ovate, triangular-ovate, or suborbicular, bases cordate, truncate, rounded, or obtuse, venation weakly palmate or 3-nerved at base, primary veins 3 or 5), and additionally from *P. ankaranensis* and *P. decidua* in its larger fruit (ca. 5 cm wide) and seeds (ca. 3 cm long) (versus fruit 2–4 cm wide, seeds ≤ 1.8 cm long).

Monoecious lianas; stems pubescent, older branches thick, woody, to 10+ mm diam, leafy stems 1.5–4.5 mm diam. **Leaves** alternate, simple; stipules triangular, 0.7–1.2 mm long, pubescent; petiole 0.8–2.2 cm long, moderately to densely pubescent, somewhat less so abaxially; blade elliptic or obovate-elliptic, 9–12.5 × 3.5–5.5 cm, L/W = 2.0–3.0, chartaceous, both surfaces sparsely pubescent with veins pubescent, base acute, margins revolute basally, serrulate, teeth glandular, apex usually acute to narrowly obtuse (sometimes rounded on proximal blades) and acuminate with tip (0.3–) 0.5–0.8 mm long; venation pinnate, secondary veins 7–9 on each side of midrib, semi-craspedodromous, tertiary veins percurrent or sometimes reticulate; stipels (1) 2, adaxial at petiole apex, elongate-knoblike to thick-linear, 0.5–1 mm long, incurved, pubescent abaxially and laterally, mostly glabrous, smooth, and appearing glandlike adaxially (often hidden); adaxial basilaminar nectaries 2, elliptic or circular, sometimes irregular in shape, 0.8–1.5 mm long, on margin, 0.5–1.5 mm from blade base, usually visible abaxially on revolute margin; abaxial laminar nectaries absent. **Inflorescences** bisexual, terminal (becoming leaf-opposed), racemose thryses, 2–4 cm long, axes pubescent; peduncle absent; pistillate flower 1, basal; staminate flowers numerous above in cymules, cymules condensed, 2–7 flowers per cymule, primary cyme axes to 2.5 mm long; bracts lanceolate or narrowly triangular-ovate, sparsely pubescent, eglandular, staminate 1.5–2.2 mm long, pistillate 2–2.5 mm long; staminate bracteoles 1–1.7 mm long, pistillate ca. 2 mm long. **Staminate flowers** (seen only in bud): pedicels jointed, ca. 4–5 mm long, sparsely pubescent, persistent part 2–3.5 mm long; bud broadly ovoid, blunt-obtuse at apex; sepals 4, narrowly ovate or lanceolate, ca. 1.5 × 0.5–0.7 mm, mostly glabrate with few scattered hairs proximally, acute at apex with thickened tip; androecium ovoid or oblong-ovoid, ca. 0.9 × 0.5 mm, comprising ca. 16 sessile anthers densely packed on a short-stalked, ellipsoid or narrowly ellipsoid receptacle; nectary absent. **Pistillate flowers** (only remnant pedicel and fruit seen): pedicels ca. 7 mm long, densely pubescent, bibracteolate proximally; sepals not seen; ovary 4-locular, 1 ovule/locule; styles not seen. **Fruits** (only immature seen) 4-lobed [or (1–) 3-lobed if seed(s) aborted], squarish in cross-section, appearing indehiscent, ca. 3.5 × 5 cm, sparsely pubescent to glabrescent, style column not seen; pedicel ca. 1 cm long, 2 mm wide, pubescent. **Seeds** (seen only in fruit longitudinal section) broadly ovoid, ca. 30 mm long, 20 mm thick, ca. 6000 mm^3 in volume ("extra-large"), dorsal surface rounded; tegmen 0.7–0.9 mm thick; testa thin, cream-colored. Figure 6.

Pollen—Tricolpate, suboblate (P/E = 0.76–0.87), polar axis ca. 25–33 µm, equatorial axis 32–38 µm; amb subcircular; colpus medium width with margins uneven and jagged, exine semitectate-reticulate, ca. 2–2.5 µm thick, evenly thickened or slighter thicker towards colpus margin, fragmented and often gemmate at the colpus margin, muri crenate (transversely ridged) to scabrate, lumina small (voucher: *Antilahimena et al. 1803,* CAN). (Fig. 1A–C).

Distribution and Habitat—This species is known from a single collection from humid evergreen forest in northeastern Madagascar, ca. 30 km northeast of Maroansetra (Fig. 7). The collection site is located about 8 km west of the Antainambalana River at an elevation of ca. 700 m in a mid-elevation area of forested hills and ridges about 1.5 km south of a tributary river. The site is now located within the Parc Naturel de Makira (established in 2012), in the central part of the park near the eastern boundary. The collection with fruit and staminate flowers was made in January.

Etymology—The specific epithet honors Patrice Antilahimena, botanist with the Missouri Botanical Garden Madagascar program, who made the only known collection of the species and the only extensive general plant collections in the very difficult to access Makira area. He has been with the program for nearly three decades and was the first Malagasy botanist to reach 10,000 plant collections.

Notes—The species is most similar to *P. randrianaivoi*, differing most conspicuously in being much more pubescent. Additionally, leaf blades are on average longer and proportionately narrower (L/W = 2.0–3.0) with a greater number of secondary veins (7–9) and more gradually acuminate apices, stipules are larger (0.7–1.2 mm long), inflorescences have a greater number of flowers per cymule (2–7), and staminate flower pedicel persistent portions are longer (2–3.5 mm long). Stipels are always present, and are thick, incurved, and distinctly pubescent adaxially and glabrous abaxially (Fig. 6C) (versus absent or present, linear to thick, and glabrous or with few hairs). Flowering collections are needed for a description of the pistillate flowers.

The holotype comprises 2 sheets clearly labelled as "sheet 1 of 2" and "sheet 2 of 2." Collection notes indicate a liana 5 m tall, with immature fruit (though the single fruit seen is likely close to full size) and green staminate flower buds.

Preliminary Conservation Status—*Plukenetia antilahimenae* is known from a single collection from Parc Naturel de Makira. Possible threats in the park include deforestation due to slash and burn agriculture and low scale mineral exploitation, however minimal deforestation was documented between 1996 and 2016 in the east central part of the park where this species in located (Goodman et al. 2018). Based on 2023 satellite photos (as seen in Google Earth Pro) the site is in undisturbed natural forest in an area of hills and ridges covered by extensive continuous forest. Although several deforested patches were seen on satellite photos on hills and ridges in the general vicinity (about 1.3 km northeast of the site [deforestation estimated in 2012], 1.6 km south of the site [2013–2018], and 300 m southeast [2017–2018]), these were very small and scattered. We suggest a preliminary IUCN conservation status of Least Concern for this species given its presence in a protected area with extensive continuous forest cover, no imminent threats in the immediate vicinity, and only very minimal deforestation in the surrounding area on hills and ridges in the park. Furthermore, the area is poorly collected, and the species almost certainly is more widespread than a single collection might suggest. However, its conservation status should be re-evaluated if deforestation increases in this part of the park.

Plukenetia randrianaivoi L.J.Gillespie, sp. nov. TYPE: MADAGASCAR. Fianarantsoa, [Atsimo-Atsinanana region], Fiv. Farafangana, Com. Ankarana, Fkt. Manombo, Forêt classée sur latérite de Sahamahitsy, RN12, Farafanfana [Farafangana] - Vangaindrano, PK 32, à 3 km W de la RN 12, 90 m, 23°01′45″S, 47°42′33″E [−23.029°, 47.709°], 9 Mar 2003, *R. Randrianaivo, J. Andriantiana, A. Ratodimanana, T. Razafindrabeaza, O. Rabezanahary & Ratiany 948* (holotype: MO (2 sheets)! [6174479, 6174480], isotypes: CAN!, P! [P04780198], TAN [photo!], US!).

Plukenetia randrianaivoi differs from *P. antilahimenae* in its stems and inflorescence axes glabrous, petioles glabrate abaxially, leaf blade abaxial surfaces glabrous, and very small stipules (0.2–0.6 mm long). It differs from *P. analameranensis, P. ankaranensis, P. decidua*, and *P. madagascariensis* in its elliptic or obovate-elliptic leaf blades with acute bases, pinnate venation with a single primary vein, and larger fruit (5–6 cm wide) and seeds (2–2.5 cm long) (versus leaf blades ovate, oblong-ovate, triangular-ovate, or suborbicular, bases cordate, truncate, rounded, or obtuse, venation weakly palmate or 3-nerved at base, primary veins 3 or 5, fruit 2–4 cm wide, seeds ≤ 1.8 cm long).

Monoecious lianas; stems glabrous, older branches thick, woody, to 8+ mm diam, leafy stems 2–5 mm diam. **Leaves** alternate, simple; stipules thick, triangular, minute, 0.2–0.6 mm long, dark brown (when dry), glabrous; petiole 1.5–3.2 cm long, glabrate abaxially, sparsely to distally moderately puberulent adaxially; blade elliptic or obovate-elliptic, (6–) 7–11 × (2.5–) 3.5–5.5 cm, L/W = 1.7–2.5, chartaceous, abaxial surface glabrous, adaxial surface glabrate with major veins sparsely puberulent, base acute to obtuse, margins revolute, conspicuously so near base, serrulate, teeth minutely glandular, apex rounded to broadly obtuse and abruptly acuminate with tip 0.5–0.9 mm long; venation pinnate, secondary veins 5–7 on each side of midrib, semi-craspedodromous, tertiary veins percurrent or sometimes reticulate; stipels absent or (1) 2, adaxial at petiole apex, slender-linear with glandular apex to elongate-knoblike, to 0.9 mm long, often incurved, glabrous or with few hairs; adaxial basilaminar nectaries 2–4, circular to oblong, often irregular in shape, 0.6–2 mm long, on or near margin, 0.5–2 mm from blade base, usually visible abaxially on revolute margin, sometimes hidden; abaxial laminar nectaries absent. **Inflorescences** bisexual or sometimes staminate, terminal (becoming leaf-opposed), racemose thryses, 1–7 cm long, axes glabrous; peduncle absent (bisexual) or 0.1–0.3 mm (staminate); pistillate flower 1, basal, or sometimes absent, staminate flowers numerous above in cymules; cymules condensed, 1–2-flowered, primary cyme axes to 1.5 mm long; bracts lanceolate or triangular-ovate, glabrous, eglandular, staminate 1.5–2.5 mm long, pistillate ca 2 mm long; staminate bracteoles ca 1 mm long, pistillate ca. 1.5 mm long. **Staminate flowers** not seen; pedicels jointed, persistent part 1–2.2 mm long. **Pistillate flowers** (only seen in very immature fruit stage): pedicels ca. 15 mm long, glabrate to sparsely puberulent, bibracteolate proximally; sepals triangular, ca. 0.7 × 0.5 mm; ovary 4-locular, 1 ovule/locule, sparsely puberulous to glabrate, 4-winged; styles completely connate into a thick-cylindric column, ca. 2.5 mm long, 1.3 mm wide at base, tapered to 0.9 mm wide at apex, glabrate; stigmas 4, deltate-suborbicular, each 0.5–0.7 mm wide. **Fruits** 4-lobed [or (1–) 3-lobed if seed(s) aborted], squarish in cross-section, apparently indehiscent, 2.5–3.5 × 5–6 cm, green to yellow, glabrous, surface verrucose, each carpel lobe carinate, keel widened centrally into small horn-like wing 0.2 cm long; style column persistent, ovoid or subspherical, ca. 2.5 mm long, 2.1–2.7 mm wide, stigmas forming a raised, often somewhat lobed ring at apex; pedicel ca. 2 cm long, 2 mm wide, glabrescent or glabrous. **Seeds** (seen only in fruit cross-section) subspherical or broadly ellipsoid, 20–25 × 20–25 × 18–23 mm, 3500–7500 mm^3 in volume ("extra-large"), ventral surface somewhat obtusely angular, dorsal surface rounded; tegmen 0.7–0.8 mm thick; testa thin, off-whitish. Figures 5, 8.

Distribution and Habitat—This species is known from two fruiting collections from low-elevation humid evergreen forest in southeastern Madagascar (Fig. 7). Collection information on *Randrianaivo 948* indicates a laterite substrate. The collection from Atsimo-Atsinanana region was made in March and that from Anosy region in October. Both collections also include old inflorescences, but no flowers remain.

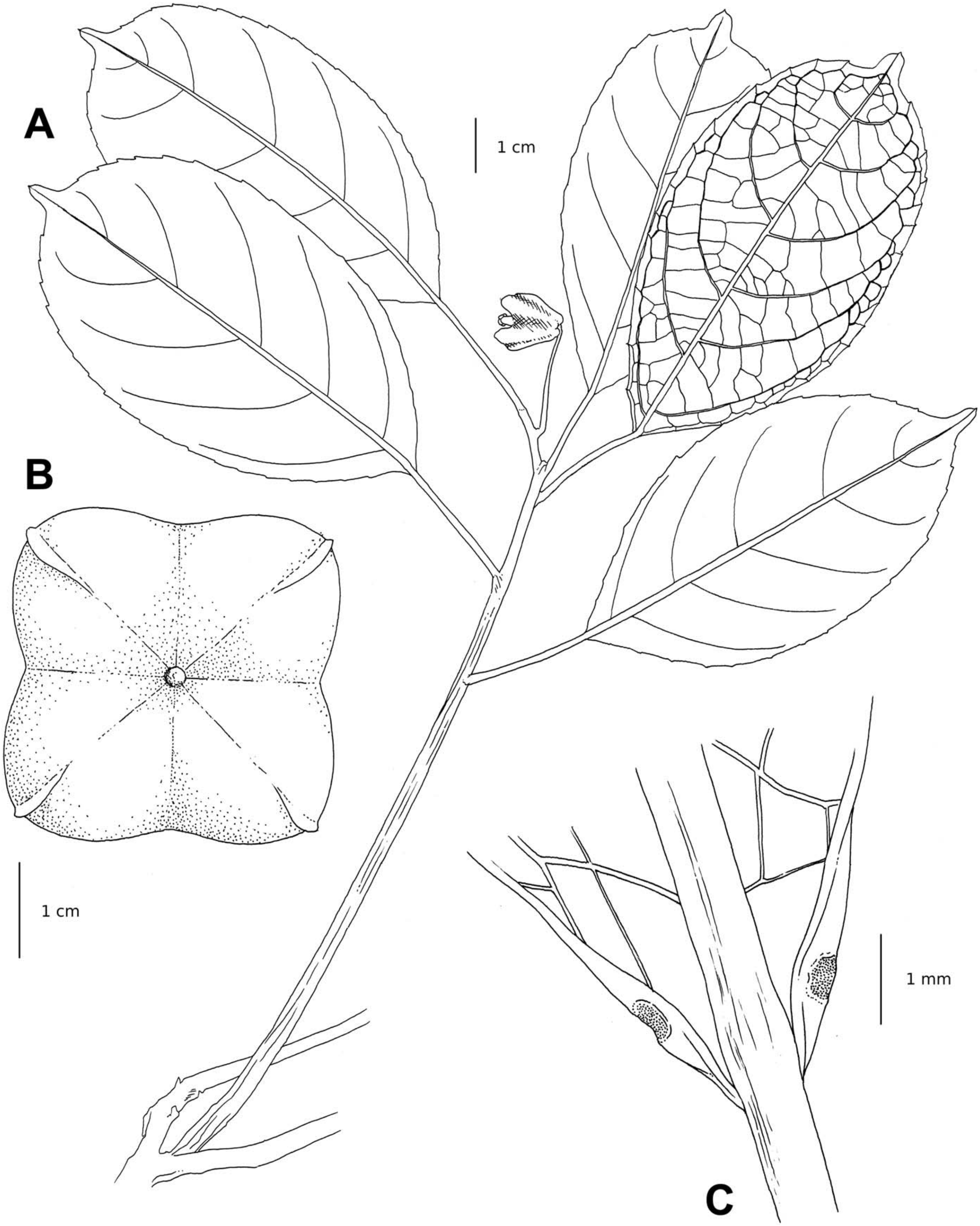


FIG. 8. *Plukenetia randrianaivoi* sp. nov., *R. Randrianaivo et al. 948* (isotype). A. Habit with immature fruit (CAN). B. Fruit (CAN). C. Leaf abaxial surface showing adaxial basilaminar nectaries on revolute margin (US). Illustration by Jessica Cosham.

Etymology—The specific epithet honors Richard Randrianaivo, botanist with the Missouri Botanical Garden Madagascar program, who made the first collection of the species.

Notes—This species is very similar to and likely most closely related to *P. antilahimenae*. The most obvious differences are the lack of pubescence on stems, inflorescence axes, and leaf blade abaxial surfaces, and the sparser shorter pubescence on the petioles and leaf blade adaxial surfaces in *P. randrianaivoi*. Leaf blades are generally more rounded at the apex with an abruptly acuminate tip, on average shorter and proportionately wider (L/W 1.7–2.5 versus 2.0–3.0 in *P. antilahimenae*), and with fewer secondary veins (5–7 versus 7–9). Additional differences include smaller stipules (0.2–0.6 mm versus 0.7–1.2 mm long), fewer flowers per cymule (1–2 versus 2–9), a shorter persistent portion of the staminate flower pedicel (1–2.2 mm versus 2–3.5 mm long). More collections of both species are needed to determine if these quantitative differences hold up once the full range of variation in each species is understood. Flowering collections are needed of *P. randrianaivoi* for complete descriptions of staminate and pistillate flowers.

One or two pairs of extrafloral nectaries are present at the base of the leaf blade on the adaxial surface as is characteristic of the genus. However, these laminar glands are generally not visible adaxially since they are on the revolute margin of the blade and are usually visible from the abaxial side or sometimes completely hidden within the rolled margin (Fig. 8C). This character is shared with *P. antilahimenae*, but in the latter the margin is often less revolute and the glands less hidden (Fig. 6B).

A pair of stipels is often present at the leaf blade-petiole adaxial junction (occasionally only a single stipel), but presence is variable both within and between collections, with *Randrianaivo et al. 948* mostly lacking stipels and *Randrianasolo et al. 1598* mostly with stipels. Distinct linear stipels were seen on only one leaf of *Randrianaivo et al. 948*, whereas some other leaves have faint knobs. *Randrianasolo et al. 1598* has stipels varying from slender-linear with a glandular apex to elongate-knoblike.

The holotype (*Randrianaivo et al. 948 MO*) comprises 2 sheets clearly labelled as sheet 1 of 2 and sheet 2 of 2 (Fig. 5A). Collection notes on the type collection indicate a climbing liana with a dbh of 3 cm and yellow fruit. Fruit (likely full size or close to) on *Randrianasolo et al. 1598* are described as green with 4 striking ridges.

Conservation Status—*Plukenetia randrianaivoi* is known from two collections in southeastern Madagascar, about 185 km apart. The northern collection (*Randrianaivo et al. 948*) was made in 2003 in remnant forest on lateritic soils about 7 km from the coast, outside (and about 300 m south of) the southern boundary of Réserve Spéciale Manombo. When LG visited the collection site area in 2012 the forest was highly degraded with a mostly low canopy (5–7 m) with some taller trees; LG and team did not find any plants of *P. randrianaivoi*. Based on satellite images (in Google Earth) extensive deforestation just south of the collection area took place between 2003 and 2013. The southern collection (*Randrianasolo et al. 1598*) was made in 2014 in the northern part of the Vohimena Range in what is now the Réserve de Ressources Naturelles de la Forêt Naturelle de Tsitongambarika (established 2015). The collection site is located in a valley on the west side of the range, at low elevation (ca. 290 m) near the western boundary of the reserve. The site is currently in a small forest fragment within an agricultural-forest mosaic zone (where forest is mostly restricted to rocky riparian areas and steep slopes) that is located between densely forested slopes in the reserve and completely deforested agricultural or secondary scrub areas outside. Considerable loss in forest cover in the vicinity of the site appears to have occurred at some point between 1985 and 2009 based on satellite images. This is consistent with an overall 8.2% loss in forest cover documented in the reserve between 1996 and 2006, mostly in low elevation areas near the reserve boundary (Goodman et al. 2018). The main threat appears to be habitat loss due mostly to slash and burn agriculture. Based on only two disjunct occurrence records with a total area of occupancy (AOO) of 8 km^2 (based on a 4 km^2 grid), corresponding to two locations, and continued decline in quality and extent of habitat at each location, we recommend that *P. randrianaivoi* be assigned a preliminary IUCN conservation status of Endangered: EN B2ab(iii).

Additional Specimens Examined—**Madagascar.**—TOLIARA: Anosy Region. Ranomafana, Mangatsiaka, Vohimena forest, Lakatomamety Stream, near Serges cassava plantation field, 291 m, 24°34′34″S, 47°02′10″E [−24.576°, 47.036°], 18 Oct 2014, *A. Randrianasolo, F. Rakotoarivony, T. Andriamihajarivo & A. Razanatsima 1598* (MO, 2 sheets; P).

KEY TO THE SPECIES OF *PLUKENETIA* SECT. *MADAGASCARIENSES*

[Adapted from Gillespie (2007) and Cardinal-McTeague and Gillespie (2020)]

1. Leaf blades elliptic or obovate-elliptic, bases acute or obtuse, venation pinnate, primary vein 1; humid evergreen forest, eastern Madagascar
    2. Stems and inflorescence axes glabrous; petioles glabrate abaxially, sparsely to moderately puberulent adaxially; leaf blade abaxial surfaces glabrous, apices rounded to broadly obtuse and abruptly acuminate; stipules 0.2–0.6 mm long . . . . *P. randrianaivoi*
    2. Stems and inflorescence axes pubescent; petioles pubescent; leaf blade abaxial surfaces sparsely pubescent with veins pubescent, apices usually acute to narrowly obtuse and more gradually acuminate; stipules 0.7–1.2 mm long . . . . *P. antilahimenae*
1. Leaf blades ovate, oblong-ovate, triangular-ovate, or suborbicular, bases cordate, truncate, rounded, or obtuse, venation weakly palmate or 3-nerved at base, primary veins 3 or 5; deciduous or semi-deciduous forest, western, far northern and far southern Madagascar
    3. Styles entirely connate, 1.8–5.5 mm long, stylar column obconic or obovoid, free style arms absent; staminate flowers with sepals 1.2–2.2 mm long, androecia to 1 mm long, anthers 15–24; inflorescences thyrses, terminal and appearing leaf-opposed, staminate flowers in condensed to lax cymules; glandular knobs absent at petiole apex.
        4. Staminate receptacle and androecium flat; indumentum hirsute (hairs 0.4–0.6 mm long); inflorescences 0.8–2 cm long; ovary with rounded wings . . . . *P. analameranensis*
        4. Staminate receptacle and androecium cylindrical; indumentum finely puberulous (hairs ca. 0.1 mm long); inflorescences (2–) 5–16 cm long; ovary with conical horns . . . . *P. ankaranensis*
    3. Styles 50–70% connate, entire style 8–16 mm long, stylar column cylindrical, free style arms slender, tapered; staminate flowers with sepals 3–6 mm long, androecia 1.6–4 mm long, anthers 18–60+; inflorescences very narrow thyrses or racemes, axillary or terminal, staminate flowers single per node or in condensed cymules; glandular knobs 1–2 at petiole apex, sometimes minute 2
        4. Inflorescences terminal racemes, staminate flowers single per node; bracts triangular, 1–2 mm long, sessile, eglandular; androecia 1.6–1.8 mm long, anthers 18–30 on ellipsoid or oblong-ellipsoid receptacle; leaf blades triangular-ovate or ovate . . . . *P. decidua*
        4. Inflorescences axillary thyrses, staminate flowers in condensed cymules; bracts lanceolate, 3–8 mm long, usually petiolate and 2–glandular; androecia 3–4 mm long, anthers 35–60 + on narrowly conical receptacle; leaf blades broadly ovate or orbicular . . . . *P. madagascariensis*

Acknowledgments

The Missouri Botanical Madagascar Program and staff are gratefully acknowledged, both for facilitating fieldwork in Madagascar in 2012 and for making their collections widely available; a special thanks to Jackie Razanatsoa for her excellent guidance and assistance in the field, and to H. Andriamaharoa and M. A. Rabevazaha for their help in looking for *P. randrianaivoi* in the Monombo area. Many thanks to Jessica Cosham and Susan Laurie-Bourque for the illustrations; Paul Sokoloff for assistance taking the pollen SEM and rehydrated flower images; Mats Hjertson for images of the UPS specimen of *Razafimandimbison et al. 416*; Lyndsey Sharpe and Paul Sokoloff for the images of CAN and MO type specimens; Olivier Lachenaud for the image of the TAN specimen of *Randrianaivo et al. 948* and for bringing to my attention the BR specimen of *Razafimandimbison et al. 416*; Geoff Levin for assistance with the map and plates; and Geoff Levin and two anonymous reviewers for their helpful comments. We thank the following herbaria and staff for facilitating visits and/or loans or for providing herbarium specimen images: BR, K, MO, P, UPS. We thank *Systematic Botany* for granting permission to reproduce Figures 2D, E, and 7F from Gillespie (2007: 784, 788) in Fig. 3A–C, and Meise Botanic Garden for permission to use the image of *Razafimandimbison et al. 416* (BR) in Fig. 4. The Canadian Museum of Nature is gratefully acknowledged for providing financial support to LG.

Author Contributions

LG carried out the taxonomic work. KW and WCM generated the DNA sequence data and WCM analyzed the data. LG and WCM prepared the figures. LG wrote the manuscript with contributions from KW and WCM.

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Appendix 1. List of species and vouchers used in the ETS+ITS phylogeny (Fig. 4), arranged by: Species. Country. Collector and number (Herbarium code), GenBank numbers for ETS and ITS. Most sequences are from Cardinal-McTeague et al. (2019), one is from Cardinal-McTeague and Gillespie (2020), and two newly published here for *P. randrianaivoi* L.J.Gillespie sp. nov. are indicated by an asterisk (*).

Ingroup: ***Plukenetia africana*** Sond. Botswana. *Palomoti 1086* (MO), MF502432, MF502515; *Pope et al. 834* (MO), MF502433, MF502516. Namibia. *Bartsch 1859* (US), MF502431, MF502513. ***P. ankaranensis*** L.J.Gillespie. Madagascar. *Gillespie et al. 10697* (CAN), MF502434, KP794438; *Lees s.n.* (CAN), MF502435, KP794437. ***P. brachybotrya*** Müll.Arg. Bolivia. *Fuentes & Torrico 5398* (MO), MF502438, MF502518. Peru. *Galiano et al. 6612* (MO), MF502439, MF502519. ***P. brevistyla*** Card.-McTeag. & L.J.Gillespie. Brazil. *Lowrie et al. 30* (MO), MH119142, —. ***P. carabiasiae*** J.Jiménez Ram. Mexico. *Meave et al. 1550* (MO), MF502441, MF502521. ***P. chocoensis*** L.J.Gillespie & Card.-McTeag. Colombia. *Gentry et al. 47799* (MO), MF502442, MF502522. ***P. conophora*** Müll.Arg. Cameroon. *Nemba & Thomas 434* (MO), MF502444, KP794457. Democratic Republic of Congo. *Hart 1621* (MO), MF502443, MF502523. ***P. corniculata*** Sm. Bangladesh. *Huq & Haroon 10780* (GH) [KW], MF502445, MF502524; (MO) [WCM], MF502446, MF502525. ***P. decidua*** L.J.Gillespie. Madagascar. *Rakotomalaza 597* (CAN), MF502447, MF502526. ***P. ×huayllabambana*** Bussmann, C.Téllez & A.Glenn. Peru. *Quipuscoa 381* (MO), MF502452, MF502531; *Tellez et al. 4* (MO), MF502454, MF502533. ***P. lehmanniana*** (Pax & K.Hoffm.) Huft & L.J.Gillespie. Ecuador. *Clark 3953* (MO), MF502460, MF502538; *Zak & Jaramillo 3401* (MO), MF502462, MF502540. ***P. loretensis*** Ule. Peru. *Vasquez & Jaramillo 3283* (MO), MF502467, MF502544; *Vasquez et al. 38069* (MO), MF502468, MF502545. ***P. madagascariensis*** Leandri. Madagascar. *Andrianjafy 1648* (CAN), MF502469, MF502546; *Gillespie 4175* (CAN), MF502470, MF502547; *Villiers et al. 4899* (MO), MF502471, MF502548. ***P. megastyla*** Card.-McTeag. & L.J.Gillespie. Bolivia. *Ledezma et al. 921* (CAN), MF502428, MF502511. Brazil. *Sperling et al. 5873* (MO), MF502429, MF502512. ***P. penninervia*** Müll.Arg. Belize. *Atha et al. 1001* (MO), MF502472, KP794455. Mexico. *Martínez 10527* (MO), MF502474, KP794456. ***P. polyadenia*** Müll.Arg. Guyana. *Wurdack 5288* (US), MF502479, MF502554. Smithsonian Greenhouse ex French Guiana. *Gillespie 4314* (CAN), MF502478, MF502553. ***P. serrata*** (Vell.) L.J.Gillespie. Brazil. *Davidse 10480* (MO), MF502480, MF502555; *Thomas 10221* (NY), MF502485, MF502559. ***P. randrianaivoi*** sp. nov. L.J.Gillespie. Madagascar. *Randrianasolo et al. 1598* (MO), OR523225*, OR519879*. ***P. stipellata*** L.J.Gillespie. Costa Rica. *Liesner 3088* (MO), MF502489, KP794451; *Morales & Rojas 5342* (MO), MF502490, KP794450. ***P. supraglandulosa*** L.J.Gillespie. Suriname. *Acevedo-Rodriguez 6022* (US), MF502493, MF502563. ***P. sylvestris*** Card.-McTeag. & L.J.Gillespie. Peru. *Monteagudo et al. 15252* (MO), MF502451, MF502530; *Woytkowski 6670* (MO), MF502458, MF502537. ***P. verrucosa*** Sm. French Guiana. *Barrabe & Crozier 145* (US), MF502494, MF502564. Suriname. *Hoffman 5917* (US), MF502496, MF502566. ***P. volubilis*** L. Ecuador. *Burnham & Krings 1640* (MO), MF502498, KP794446. Smithsonian Greenhouse ex Peru. *Wurdack s.n.* (US), MF502506, MF502572.

Outgroup: ***Haematostemon guianensis*** Sandwith. Guyana. *Wurdack 4350* (US), MF502427, KP794434. ***Romanoa tamnoides*** (A.Juss.) Radcl.-Sm. Bolivia. *Fuentes 1848* (MO), MF502507, MF502573; *Raes & Terceros 177* (MO), MF502508, KP794435.