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A Revised Sectional Classification of *Plukenetia* L. (Euphorbiaceae, Acalyphoideae) with Four New Species from South America

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Abstract—We present a phylogenetic classification for *Plukenetia* (Euphorbiaceae, Acalyphoideae) based on morphology and molecular phylogenetic studies using nuclear (ETS, ITS, *KEA1* introns 11 and 17, *TEB* exon 17) and plastid (*matK*, *ndhF*, *psbA-trnH*) DNA data. *Plukenetia* comprises 25 species divided into six sections, with three new sections and four new species described here. The circumscription of *Plukenetia* is unaltered from recent treatments and we continue to recognize *Romanoa* as distinct. The sections of *Plukenetia* correspond with the subclade system proposed by Cardinal-McTeague and Gillespie (2016): P1 = *P.* sect. *Fragariopsis* comb. et stat. nov.; P2 = *P.* sect. *Penninerviae* sect. nov.; P3 = *P.* sect. *Plukenetia*; P4 = *P.* sect. *Angostylium*; and P5 = *P.* sect. *Hedraiostylus* + *P.* sect. *Madagascarienses* sect. nov. The sections are distinguished by a combination of leaf venation, staminate flower morphology, pistillate flower number, style morphology, fruit type, and seed size. Additionally, we describe three new species from South America belonging to sect. *Penninerviae*: *Plukenetia brevistyla* and *Plukenetia megastyla* from the Amazon basin and *Plukenetia chocoensis* from the Chocó Biogeographic Region of Colombia. The new Amazonian species are morphologically similar to *P. brachybotrya* but distinguished by their style shape and size. The new Colombian species is morphologically similar to *P. penninervia* but distinguished by its elongate basilar extrafloral nectaries, presence of abaxial laminar extrafloral nectaries, and longer inflorescences. We also describe a new species from sect. *Plukenetia*, *Plukenetia sylvestris*, which is found in central and southern Peru. This species is suggested to be the wild progenitor of the cultivated *P. carolis-vegae*, differing by its smaller seeds/fruits and fewer stamens. Molecular data, including a new ETS phylogeny sampling *P. brevistyla*, support our new taxa as distinct. Keys to the sections and species of *Plukenetia* are provided and we designate 12 new lectotypes for *Plukenetia* and *Romanoa*.

Keywords—Euphorbiaceae, lectotypes, molecular phylogeny, *Romanoa*, taxonomy.

The circumscription of *Plukenetia* L. (Euphorbiaceae tribe Plukenetieae) has changed considerably over the last four centuries, particularly in repeated shifts between recognizing multiple genera and a single morphologically diverse pantropical genus. The genus was named *Plukenetia* by French botanist Charles Plumier (1703) to honour English botanist Leonard Plukenet, who is regarded for his influential publications on New World plants, *Phytographia* vols. 1–4 (Plukenet 1691a, 1691b, 1692, 1696a) and *Almagestum botanicum* (Plukenet 1696b). Plumier's name was later validated by Linnaeus (1753) as *Plukenetia* and was chosen over a second pre-Linnaean genus from Southeast Asia, *Sajor* Rumph. (type = *Plukenetia corniculata* Sm.). *Plukenetia* now comprises 25 species of non-stinging twining lianas, vines, and rarely subshrubs. The most well known species, *P. volubilis* L. (Sacha Inchi or Inca Peanut), has been traditionally cultivated in Peru for its oil-rich seeds, which have gained in popularity and consumption over the past 20 yr (e.g. Bussmann et al. 2013; Kodahl 2020). The genus was most recently revised by Gillespie (1993, 2007) and outside of those treatments three new species have been described, one from Oaxaca, Mexico (Jiménez Ramírez 1993) and two from the Andes of northern Peru (Bussmann et al. 2009, 2013). A recent phylogenetic study resolved most relationships in *Plukenetia* and analyzed the historical biogeography and seed size evolution of the genus (Cardinal-McTeague et al. 2019a). Here, we use those phylogenetic hypotheses to present a revised sectional classification and updated species list for *Plukenetia*, including four new species from South America, one of them hypothesized to be the wild progenitor of the cultivated species *P. carolis-vegae*.

Plukenetia is a member of tribe Plukenetieae, a distinctive lineage in Euphorbiaceae noted for its twining vine growth forms and stinging hair defenses (Webster 1994, 2014; Wurdack et al. 2005; Cardinal-McTeague and Gillespie 2016).

Plukenetia belongs to the non-stinging subtribe Plukenetiinae, which is divided into two informal groups comprising rare small tree and shrub genera (*Angostylis*, *Astrococcus*, and *Haematostemon*) and twining vine and liana genera (*Plukenetia* and *Romanoa*) (Gillespie 1994; Cardinal-McTeague and Gillespie 2016). The other genera of Plukenetiinae contain only one or two species each, making *Plukenetia* the most diverse and species-rich member of the clade. *Plukenetia* is readily distinguished by the combination of 4-carpellate fruits/ovaries (compared to 3-carpellate in other Plukenetieae and most other Euphorbiaceae) and the presence of paired basilar extrafloral nectaries (often called 'glands') located on the adaxial surface of the leaf blade near or just above the petiole (Gillespie 1993, 2007).

History of Generic and Sectional Classifications—The early taxonomic history of *Plukenetia* was complicated by the creation of multiple generic names for the same taxon (Table 1). In particular, several genera were described for *P. corniculata* Sm. (*Sajor* Rumph., nom. inval. pre 1753, *Pterococcus* Hassk., nom. cons., *Hedraiostylus* Hassk., *Ceratococcus* Meisn., nom. illeg., *Sajorium* Endl., nom. illeg.) and for *P. serrata* (Vell.) L.J. Gillespie (*Vigia* Vell., *Fragariopsis* A.St.-Hil., *Accia* A.St.-Hil., *Botryanthe* Klotzsch).

Baillon (1858) was the first to recognize a broader circumscription for *Plukenetia* and unified three previously distinct genera under Endlicher's (1843) illegitimate replacement name *Sajorium* (Table 1). Müller (1864, 1865, 1866) built on Baillon's classification but applied it under the earliest legitimate genus, *Plukenetia*. Müller's work provided many of the sectional names used today (Table 1). However, Müller mistakenly described *P. peruviana* Müll.Arg., a synonym of the type species *P. volubilis*, and placed each in two different sections. The type species of *Plukenetia*, *P. volubilis*, was placed in sect. *Euplukenetia* alongside most other neotropical species known

TABLE 1. Generic and sectional classifications of *Plukenetia* and *Romanoa* (NWSG2 = New World species group "2"; ^a = genera described by Pax and Hoffmann 1919; names in [hard brackets] predate Linnaean taxonomy and are provided for context).

Molecular phylogeny	Prior to Baillon	Baillon (1858)	Müller (1864, 1865, 1866)	Pax and Hoffmann (1919)	Webster (1975)	Gillespie (1993, 2007)	This treatment
<i>Plukenetia</i> subclade P1	<i>Vigia</i> (Vell. 1832) <i>Fragariopsis</i> (A.St.-Hil. 1840) <i>Accia</i> (A.St.-Hil. 1840) <i>Botryanthe</i> (Klotzsch 1841)	<i>Fragariopsis</i>	<i>Fragariopsis</i>	<i>Fragariopsis</i>	<i>Fragariopsis</i>	NWSG2	<i>P.</i> sect. <i>Fragariopsis</i> comb. et stat. nov.
<i>Plukenetia</i> subclade P2	<i>Plukenetia</i> (L. 1753)	<i>Sajorium</i> sect. <i>Pluknetia</i>	<i>P.</i> sect. <i>Euplukenetia</i>	<i>P.</i> sect. <i>Euplukenetia</i> <i>Apodandra</i> ^a	<i>Plukenetia</i>	NWSG2	<i>P.</i> sect. <i>Penninerviae</i> sect. nov.
<i>Plukenetia</i> subclade P3	[<i>Pluknetia</i> (Plum. 1703)] <i>Plukenetia</i> (L. 1753)	<i>Sajorium</i> sect. <i>Pluknetia</i>	<i>P.</i> sect. <i>Euplukenetia</i> <i>P.</i> sect. <i>Cylindrophora</i>	<i>P.</i> sect. <i>Cylindrophora</i> <i>Eleutherostigma</i> ^a <i>Elaeophora</i> (Ducke 1925)	<i>Plukenetia</i> <i>Eleutherostigma</i> ^a	<i>P.</i> sect. <i>Plukenetia</i>	<i>P.</i> sect. <i>Plukenetia</i>
<i>Plukenetia</i> subclade P4	n/a	n/a	<i>P.</i> sect. <i>Angostylidium</i>	<i>Tetracarpidium</i> (Pax 1899) <i>Angostylidium</i> ^a	<i>Plukenetia</i>	<i>P.</i> sect. <i>Angostylidium</i>	<i>P.</i> sect. <i>Angostylidium</i>
<i>Plukenetia</i> subclade P5	[<i>Sajor</i> (Rumph. 1750)] <i>Pterococcus</i> (Hassk. 1842) <i>Hedraiostylus</i> (Hassk. 1843) <i>Ceratococcus</i> (Meisn. 1843) <i>Sajorium</i> (Endl. 1843)	<i>Sajorium</i> sect. <i>Hedraiostylus</i>	<i>P.</i> sect. <i>Sajor</i> <i>P.</i> sect. <i>Hedraiostylus</i>	<i>Pseudotragia</i> (Pax 1908) <i>Pterococcus</i>	<i>Plukenetia</i>	<i>P.</i> sect. <i>Hedraiostylus</i>	<i>P.</i> sect. <i>Hedraiostylus</i>
<i>Plukenetia</i> subclade P5	n/a	n/a	n/a	n/a	<i>Plukenetia</i>	Madagascan species group	<i>P.</i> sect. <i>Madagascarienses</i> sect. nov.
<i>Romanoa</i>	<i>Anabaena</i> (A.Juss. 1824) <i>Romanoa</i> (Trev. 1848)	<i>Sajorium</i> sect. <i>Anabaena</i>	<i>P.</i> sect. <i>Anabaena</i>	<i>Anabaenella</i> ^a	<i>Anabaena</i>	<i>Romanoa</i>	<i>Romanoa</i>

at the time (*P. brachybotrya*, *P. penninervia*, and *P. verrucosa*). The synonym, *P. peruviana*, was placed its own sect. *Cylindrophora* on the basis of having a long cylindrical stylar column, despite sharing this exact morphology with *P. volubilis*. Even after the synonymy of *P. peruviana* with *P. volubilis* was identified, Pax and Hoffmann (1919) perpetuated this confusion by placing *P. volubilis* in sect. *Cylindrophora* (= sect. *Plukenetia*) and misapplying sect. *Euplukenetia* (= sect. *Penninerviae* sect. nov.) to a subset of neotropical species united by short connate styles and mostly pinnately veined leaves (*P. brachybotrya*, *P. penninervia*, *P. verrucosa*) even though it excluded the type for the genus.

Both Baillon and Müller upheld *Fragariopsis* (= *P. serrata*) as a distinct genus, Baillon (1858) for its unique androecium morphology, high and variable stamen count, and thick stylar columns, and Müller (1866) because it had fleshy indehiscent fruits rather than dry dehiscent capsules. High stamen number, thick stylar columns, and fleshy fruits would be shared with subsequently described species of *Plukenetia*, but its androecium morphology remains distinct.

Five decades after Baillon and Müller, Pax (1899, 1908) and Pax and Hoffmann (1919) dismantled *Plukenetia* and in the process described several new genera (Table 1). Many genera in the Pax and Hoffmann (1919) treatment were poorly defined and included obvious errors, such as placing *P. brachybotrya* in sect. *Euplukenetia* (= sect. *Penninerviae* sect. nov.) and its synonym *P. buchtienii* in their new genus *Apodandra*. Over time, Croizat (1941), Webster (1975, 1994), and Gillespie (1993, 1994, 2007) challenged Pax and Hoffmann's treatment,

reuniting these genera under *Plukenetia* on the basis of their numerous overlapping characters and synapomorphic 4-carpellate ovaries.

Analyses of leaf, floral, and pollen morphology provided many characters to develop species group hypotheses in *Plukenetia* (Gillespie 1993, 1994, 2007), but major taxonomic changes were withheld pending molecular phylogenetic study. Recent phylogenetic analyses (Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019a) support many of Gillespie's hypotheses and provide a robust framework to formalize a revised classification for *Plukenetia* (Fig. 1; Tables 1, 2).

Taxonomically Informative Characters—In the phylogeny of Cardinal-McTeague et al. (2019a), *Plukenetia* was divided into two major clades, the pinnately veined clade (subclades P1 + P2) and the palmately veined clade (subclades P3–P5) (Fig. 1). These clades are united by their leaf blade venation, with 1 primary vein in the pinnately veined clade (3-veined in *P. verrucosa*) and 3(–5) primary veins in the palmately veined clade. The pinnately veined clade was previously called New World species group "2" (sensu Gillespie 1993) and was determined to be further united by entirely connate styles, all or mostly sessile anthers, and coarsely reticulate pollen tecta. Some Old World species in the palmately veined clade share entirely connate styles (*P. ankaranensis*, *P. corniculata*) and sessile anthers (species in Madagascar), rendering those characters non-exclusive to the pinnately veined clade. In addition to leaf venation, members of the palmately veined clade are united by foveolate pollen tecta.

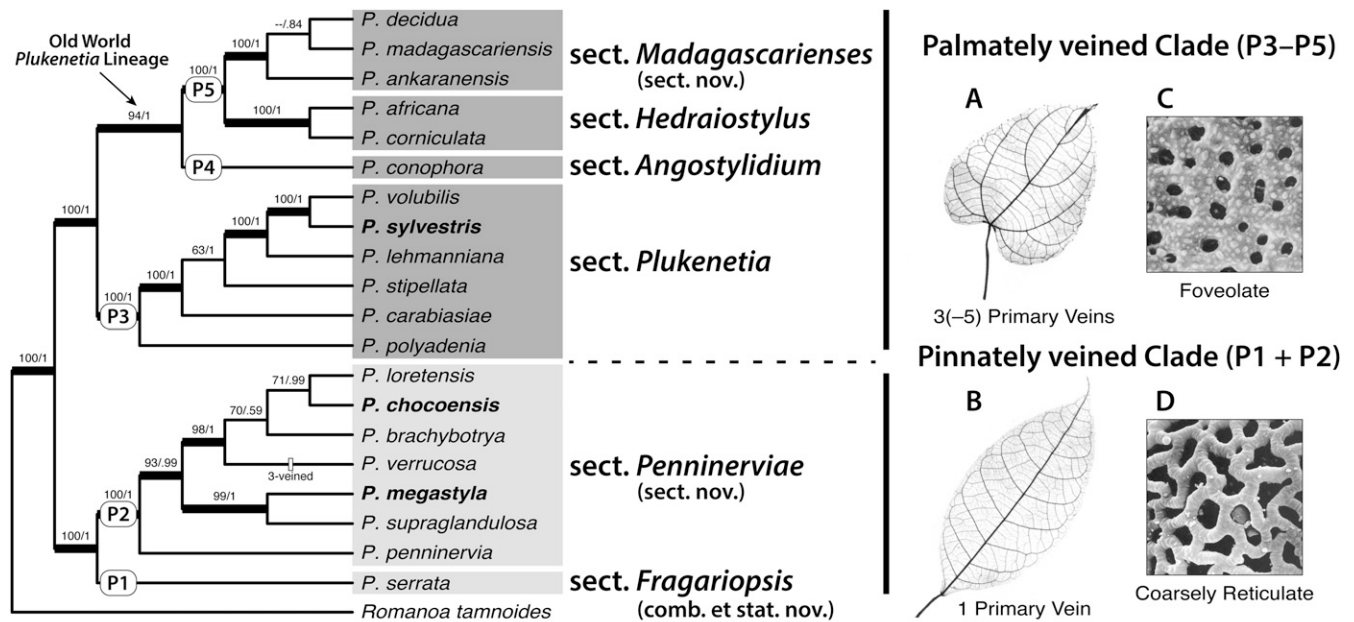


FIG. 1. Summary cladogram of the relationships recovered by Bayesian analysis of combined and partitioned ETS, ITS, *KEA1* introns 11 and 17, *TEB* exon 17, *matK*, and *ndhF* DNA sequence data of *Plukenetia* and *Romanoa* (modified from Cardinal-McTeague et al. 2019a), highlighting our revised sectional classification of *Plukenetia*. Maximum parsimony bootstrap percentage (MPBP) and Bayesian posterior probability (BPP) support values > 50% are indicated on each branch. Branches in bold indicate strong support (≥ 85 MPBP and ≥ 0.95 BPP). Subclade numbering system (P1–P5) follows Cardinal-McTeague and Gillespie (2016). Sections in the pinnately veined clade (P1 + P2) are indicated by light grey boxes; sections in the palmately veined clade (P3–P5) by dark grey boxes; new species are indicated in bold. A–B. Leaf clearings demonstrating leaf architecture (images from Gillespie 1993). A. *P. stipellata*, Gillespie 413 US. B. *P. supraglandulosa*, Granville 3626 CAY. C–D. Scanning electron micrographs demonstrating pollen tectum morphology (images from Gillespie 1994). C. *P. stipellata*, Gillespie 418 DAV. D. *P. lorentensis*, Maguire & Politi 27371 US.

A combination of staminate flower morphology, style morphology, fruit type, and seed size can be used to differentiate the sections (Table 3). Useful staminate flower characters include the presence of filaments and nectaries, nectary type, and receptacle shape (Fig. 2). Style size and morphology varies considerably, with styles ranging from partly to entirely connate, and stylar columns either cylindrical or variously shaped (Fig. 3). Seeds range from “small” ($\sim 5 \times 5 \times 4$ mm) to “medium”, “large”, “extra-large”, and “maximum” ($\sim 50 \times 35 \times 30$ mm) sized (for more detail see Cardinal-McTeague et al. 2019a). Smaller seeds (“small”, “medium”, “large”) tend to be associated with dry dehiscent capsules,

while larger seeds (“large”, “extra-large”, “maximum”) are from fleshy indehiscent berries or dry semi-dehiscent capsules.

MATERIALS AND METHODS

Morphology—Sectional descriptions of *Plukenetia* build on previous treatments (Gillespie 1993, 2007) and more recent new species descriptions (Jiménez Ramírez 1993; Bussmann et al. 2009, 2013). Herbarium material from CAN, GH, MO, NY, and US was consulted for morphology. Pollen morphology and measurement data are based on Gillespie (1993, 1994, 2007) and Nowicke and Takahashi (2002). Pollen morphology for new taxa was investigated by soaking staminate flowers with a simple rehydrating solution (100 mL water with a drop of liquid soap), isolating pollen grains

TABLE 2. Revised sectional classification of *Plukenetia* with species number, distribution, habitat, and growth forms of each section, including *Romanoa*.

Taxon	Species	Distribution	Habitat	Growth form
<i>P. sect. Angostyliidium</i>	1	Central and Western Africa	Lowland forest	Canopy lianas; stems thick
<i>P. sect. Fragariopsis</i> comb. et stat. nov.	1	Atlantic Forest of Brazil	Pre-montane to montane forest edges	Lianas; stems slender to thick
<i>P. sect. Hedraiostylus</i>	3	Southern Africa, Southeast Asia	Lowland forest edges and light gaps or savanna woodland on sandy soil	Vines, lianas, or herbs; stems slender, twining or procumbent
<i>P. sect. Madagascarienses</i> sect. nov.	3	Madagascar	Forest on limestone or spiny forest scrub	Lianas; stems slender to thick
<i>P. sect. Penninerviae</i> sect. nov.	9	Mexico, Central America, northwestern and Amazonian South America, and the Lesser Antilles	Lowland to pre-montane (montane) forest edges, rocky outcrops, and light gaps or white sand forest	Vines or lianas; stems slender
<i>P. sect. Plukenetia</i>	8	Mexico, Central America, northwestern and Amazonian South America, and the Lesser Antilles	Lowland to pre-montane forest edges, ravines, and light gaps	Vines, lianas, or canopy lianas; stems slender to thick
<i>Romanoa</i>	1	Atlantic Forest of Brazil and southwest Amazon (Bolivia, Brazil, Paraguay)	Lowland forest, rocky outcrops, and light gaps or stony soil coating	Vines or lianas; stems slender

TABLE 3. Morphological differences between the sections of *Plukenetia*, including *Romanoa*.

Taxon	Primary veins	Pistillate flowers	Staminate receptacles	Staminate nectaries	Filament length	Pollen tecta	Carpels	Style connation	Style length	Stylar column shape	Fruit type	Fruit diameter	Seed size
<i>P. sect. Angostyliidium</i>	3	1-2(3)	Subglobose	Interstaminal	< 0.5 mm	Foveolate	4	75(-90)%	4-7.5 mm	Funnel-shaped	Fleshy	4.5-7.5 cm	XL
<i>P. sect. Fragariopsis</i> comb. et stat. nov.	1	1-10	Globose	Absent	Absent	Coarsely reticulate	4	Entire	3-3.5 mm	Obovoid	Fleshy	4-5 cm	L
<i>P. sect. Hedritostylus</i>	3(-5)	1	Convex, subglobose, or globose	Absent	< 0.5 mm	Foveolate	4	~70% or entire	0.5-1.8 mm	Cylindrical or depressed-globose	Dry	1.1-2 cm	S, M
<i>P. sect. Madagascartenses</i> sect. nov.	3(-5)	1 or 1-2(3)	Ellipsoid, oblong-cylindrical, or ovoid-conical	Absent	Absent	Foveolate	4	55-60% or entire	3.5-16 mm	Cylindrical or obconic or obovoid	Dry	2.3-4 cm	L
<i>P. sect. Penninerinae</i> sect. nov.	1(3)	1	Subglobose or globose	Absent or extrastaminal	Absent, sometimes with an outer whorl 0.2-1 mm	Coarsely reticulate	4	Entire	0.3-4.5 mm	Cylindrical, depressed-subglobose, globose, obovoid, or oblong-obovoid	Dry	0.9-1.5 cm	S
<i>P. sect. Plukenetia</i>	3	1 or 1-4	Convex or subglobose	Interstaminal (absent)	0.5-3 mm	Foveolate	4	(20-40) 70-95%	5.6-35 mm	Cylindrical	Dry or fleshy	3.5-11 cm	M, L, XL, Max
<i>Romanoa</i>	3-5	1	Subglobose	Absent	0.5-1 mm	Fossulate-foveolate	3	70-80%	5.6-10 mm	Cylindrical	Dry	1-1.7 cm	S

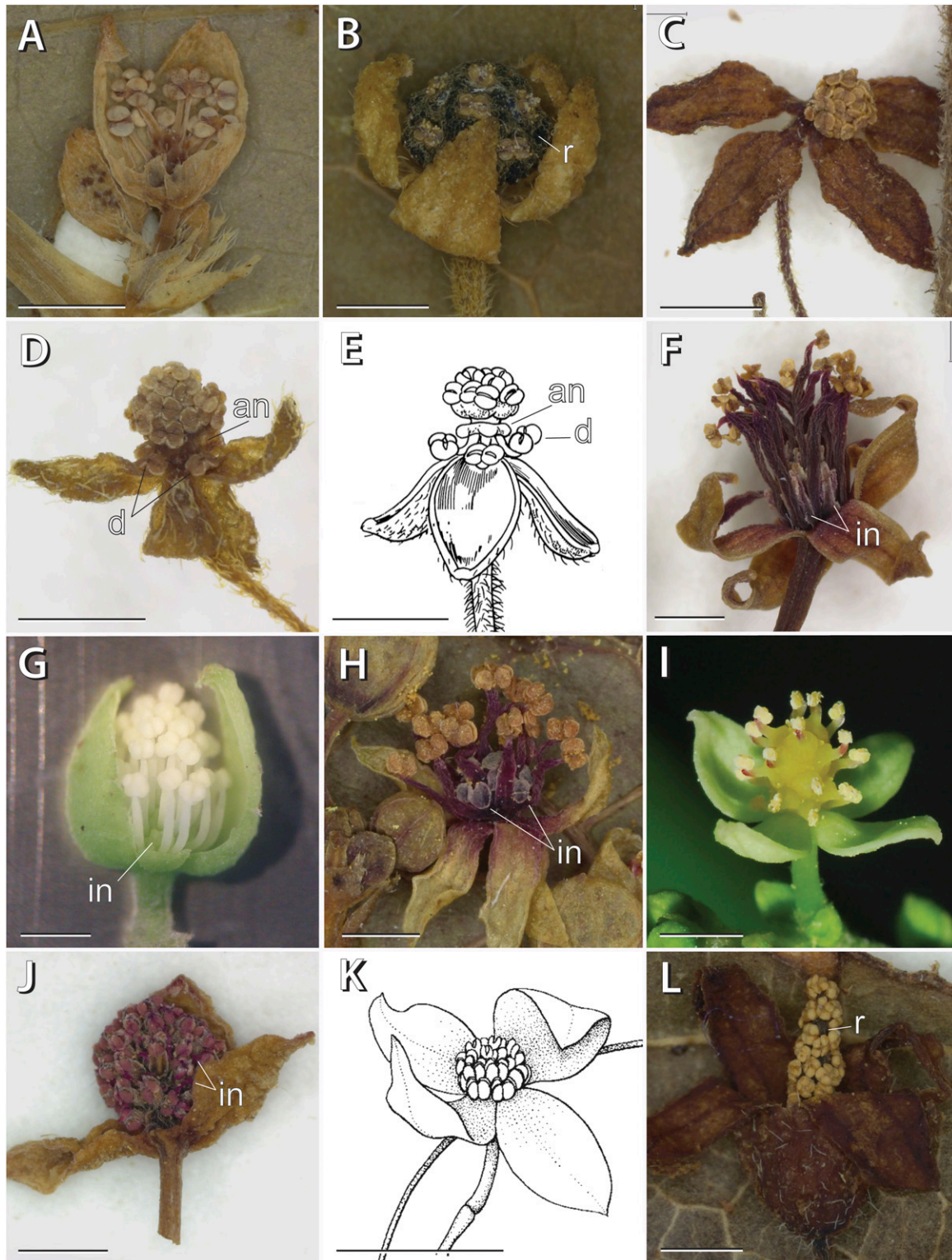


FIG. 2. Representative staminate flower diversity of *Plukenetia* and its sister genus *Romanoa*. A. *Romanoa tamnoides* (Krapovickas & Schinini 36265 MO), stamens with slender-cylindrical filaments. B. *P.* sect. *Fragariopsis*: *P. serrata* (Davidse et al. 10480 MO), anthers sessile and loosely packed on a large globose receptacle. C–E. *P.* sect. *Pemminerioia*: C. *P. lorentensis* (Freitas et al. 155 MO), anthers sessile and densely packed on a small globose receptacle; D. *P. pemminerioia* (van der Werff et al. 3173 MO), and E. *P. supraglandulosa* (Granville 3626 CAY, US), most anthers sessile and densely packed on a small globose receptacle, with a dimorphic outer whorl of ~4 stamens with filaments, and often with a 4-lobed annular nectary. F–I. *P.* sect. *Plukenetia*: F. *P. polyadenia* (Croat et al. 20285 MO), stamens with slender-cylindrical filaments and ligulate interstaminal nectaries; G. *P. stipellata* (Cardinal-McTeague 8 CAN), stamens with slender-cylindrical filaments and small irregularly shaped interstaminal nectary segments; H. *P. sylvestris* (Woytkowski 6670 MO), stamens with slender filaments and large irregularly shaped interstaminal nectary segments; I. *P. volubilis* (Wurdack s.n. US), stamens with short-conical filaments. J. *P.* sect. *Angostyliidium*: *P. conophora* (Avio et al. 1621 MO), stamens with short-conical filaments and slender-cylindrical interstaminal nectaries (in pink). K. *P.* sect. *Hedmiostylus*: *P. corniculata* (Chin See Chung 2712 L), stamens with short-conical filaments (sometimes appearing sessile). L. *P.* sect. *Madagascariensis*: *P. madagascariensis* (Villiers et al. 4889 MO), anthers more or less sessile, densely to somewhat loosely packed on an elongate receptacle. Photos A–D, F–H, J, L by W. Cardinal-McTeague; I by K. Wurdack. Line drawings: E by Alice Tangerini, K by Anita Walsmit Sachs, used with permission from the Naturalis Biodiversity Center, Leiden, Netherlands. (Abbreviations: an = annular nectary; d = dimorphic filamentous stamens; in = interstaminal nectaries; r = receptacle. Scale bars = 1 mm).

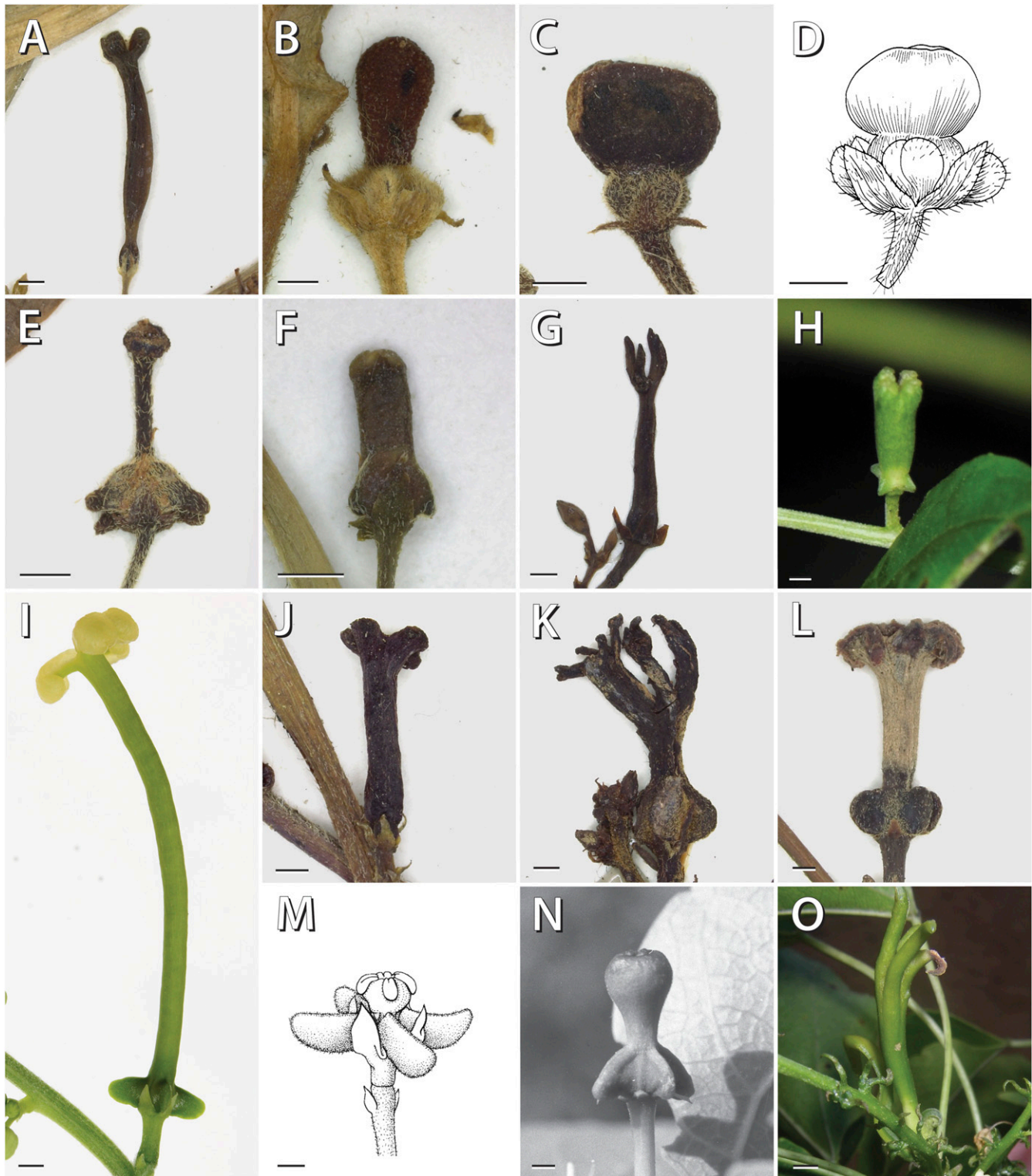


FIG. 3. Representative pistillate flower diversity of *Plukenetia* and its sister genus *Romanoa*. A. *Romanoa tamnoides* (Krapovickas & Schinini 36265 MO), styles 70–80% connate into a cylindrical column. B. *P.* sect. *Fragariopsis*: *P. serrata* (Davidse et al. 10480 MO), styles entirely connate into an obovoid column. C–F. *P.* sect. *Penminervia*: C. *P. brachybotrya* (Fuentes et al. 5398 MO) and D. *P. verrucosa* (Prance et al. 11255 DAV), styles entirely connate into a globose column; E. *P. lorentensis* (Silva et al. 4750 MO), styles entirely connate into a slender-cylindrical column, dilated at the apex; F. *P. penminervia* (Wallnöfer et al. 5996 MO), styles entirely connate into a stout-cylindrical column. G–K. *P.* sect. *Plukenetia*: G. *P. polyadenia* (Aulestia & Grefa 230 MO), H. *P. stipellata* (Cardinal-McTeague 8 CAN), I. *P. volubilis* (Wurdack s.n. US), and J. *P. sylvestris* (Woykowsky 6670 MO), styles 70–95% connate into a cylindrical column; K. *P. lehmanniana* (Rangel et al. 5734 MO), styles 20–25% connate into a cylindrical column, free style arms 2-fid near the tips. L. *P.* sect. *Angostyliidium*: *P. conophora* (Thomas 5455 MO), styles 75–(90)% connate into a funnel-shaped column, free style arms conspicuously dilated and spreading. M. *P.* sect. *Hedraiostylus*: *P. corniculata* (Brink 5771 L), styles entirely connate into a depressed-globose column with cross-shaped stigmas. N–O. *P.* sect. *Madagascarienses*: N. *P. ankaranensis* (Gillespie 4076 CAN), styles entirely connate into an obconic or obovoid column; O. *P. madagascariensis* (Andrianjafy et al. 1648 MO), styles 55–60% connate into a cylindrical column, free style arms slender and tapered. Photos A–C, E–H, J–L, by W. Cardinal-McTeague, I by K. Wurdack, N by L. Gillespie, O by P. Phillipson. Line drawings: D by Cathy Pasquale, K by Anita Walsmit Sachs, used with permission from Naturalis Biodiversity Center, Leiden, Netherlands. (Scale bars = 1 mm).

conducted in MrBayes v. 3.2.6 on XSEDE (Ronquist et al. 2012), implementing two independent MCMC runs, each with four chains, run for five million generations, and sampling every 1000 generations. We applied a single model of nucleotide evolution on an unpartitioned dataset, selected using the Akaike information criterion (AIC) following default ML Best tree searches conducted in jModelTest2 on XSEDE (Darriba et al. 2012). Independent BI MCMC runs were considered converged after the standard deviation of split frequencies was < 0.05, effective sample sizes (ESS) were > 200, and potential scale reduction factors (PSRF) were ~1.00, all as reported in MrBayes. A 25% burn-in was used prior to summarizing parameter and tree statistics and a 50% majority rule consensus tree.

Distribution Map—The base of a species distribution map was created using ggmap v. 3.0.0 (Kahle and Wickham 2013) and ggplot2 v. 3.2.1 (Wickham 2009) in R. The R script is available on Dryad (Cardinal-McTeague and Gillespie 2020).

Taxonomy—To be transparent about our methodology, the representation of taxonomic authorities may differ from previous publications by employing ICN 2017 Art. 41.4 (Turland et al. 2018), which (prior to 1 January 1953) recognizes an author's presumed intent to cite a basionym even if it had not been done in the publication of their new combination. Herbarium acronyms follow Index Herbariorum (Thiers 2019).

RESULTS

Dataset Characteristics and Phylogenetic Relationships—In total 84 accessions were included in our ETS dataset (Appendix 1), resulting in an aligned length of 469 characters (228 constant, 241 variable, 199 [42.4%] parsimony informative). AIC

identified TrN + I + G as the optimal model of molecular evolution; however, we selected the next best model that could be implemented in MrBayes, HKY + I + G (AIC delta = 1.6812). Our alignment and MrBayes tree file are available on Dryad (Cardinal-McTeague and Gillespie 2020).

The BI consensus tree is presented with ML bootstrap percentage (MLBP) and Bayesian posterior probability (BPP) support values in Fig. 4. Evidence of strong branch support was interpreted as ≥ 80 MLBP and ≥ 0.95 BPP, indicated by bold branches. The ETS phylogeny is mostly congruent with the topology of the combined seven marker dataset recovered in Cardinal-McTeague et al. (2019a), with the exception of subclade P4 moderately supported as embedded in subclade P3 (Fig. 4; MLBP = 69, BPP = 0.97).

Plukenetia brevistyla (previously unsampled) was recovered in subclade P2 as the earliest diverging lineage in a strongly supported clade sister to *P. penninervia* (Fig. 4; MLBP = 84, BPP = 0.97). Accessions of *P. megastyla* were strongly supported as monophyletic (MLBP = 100, BPP = 1) and were resolved in a weakly supported clade (MLBP = 60, BPP = 0.8) composed of a functional polytomy with the remaining species of subclade P2. Our other proposed taxa, *P. chocoensis* and *P. sylvestris*, were not well resolved when analyzed with ETS alone (Fig. 4) but were monophyletic and/or recovered as distinct with strong to moderate support when additional molecular markers were sampled (Cardinal-McTeague et al. 2019a).

TAXONOMIC TREATMENT

KEY TO THE GENERA OF NON-STINGING VINES AND LIANAS IN TRIBE PLUKENETIEAE

1. Carpels 3; leaf venation palmate, primary veins 3–5; styles partly connate into a \pm cylindrical column, 5.6–10 mm long; staminate sepals 5, stamens 10, filaments slender-cylindrical; pollen tecta fossulate-foveolate; distributed in Bolivia, southeast Brazil, and Paraguay. *Romanoa*
1. Carpels 4 (sometimes 5–7 in cultivated forms); leaf venation pinnate or palmate, primary veins 1 or 3(–5); styles entirely connate into a \pm cylindrical, depressed-subglobose, globose, obconic, obovoid, or oblong-obovoid column, 0.3–5.5 mm long, or partly connate into a cylindrical column, 1–35 mm long; staminate sepals 3–5, stamens 6–60, filaments absent, short-conical, or slender-cylindrical; pollen tecta coarsely reticulate or foveolate; distributed pantropically. *Plukenetia*

Plukenetia L., Sp. Pl. 1 (2): 1192. 1753. TYPE: *Plukenetia volubilis* L.

Vigia Vell., Fl. Flumin. Icon. 9: t.128. 1832. TYPE: *Vigia serrata* Vell. [= *Plukenetia serrata* (Vell.) L.J.Gillespie].

Fragariopsis A.St.-Hil., Leçons Bot. 426. 1840. TYPE: *Fragariopsis scandens* A.St.-Hil. [= *Plukenetia serrata* (Vell.) L.J.Gillespie].

Accia A.St.-Hil., Leçons Bot. 499. 1840, nom. illeg. TYPE: *Accia scandens* A.St.-Hil. [= *Plukenetia serrata* (Vell.) L.J.Gillespie].

Botryanthe Klotzsch, Arch. Naturgesch. (Berlin) 7: 190. 1841. TYPE (lectotype designated by Webster 1994): *Botryanthe discolor* Klotzsch [= *Plukenetia serrata* (Vell.) L.J.Gillespie].

Pterococcus Hassk., Flora 25 (2, Bleibl.): 41. 1842, nom. cons., non Pall. 1773. TYPE: *Pterococcus glaberrimus* Hassk. [= *Plukenetia corniculata* Sm.].

Hedraiostylus Hassk., Tijdschr. Natuurl. Gesch. Physiol. 10: 141. [–September] 1843. TYPE: *Hedraiostylus glaberrimus* Hassk. [= *Plukenetia corniculata* Sm.].

Sajorium Endl., Gen. Pl. Suppl. 3: 98. [October] 1843, nom. illeg. TYPE (lectotype designated by Dietrich 1852): *Sajorium corniculatum* (Sm.) D.Dietr. [= *Plukenetia corniculata* Sm.].

Ceratococcus Meisn., Pl. Vasc. Gen. 2: 369. [2–4 November] 1843, nom. illeg. TYPE: not designated.

Tetracarpidium Pax, Bot. Jahrb. Syst. 26 (3–4): 329. 1899. TYPE: *Tetracarpidium staudtii* Pax [= *Plukenetia conophora* Müll.Arg.].

Pseudotragia Pax, Bull. Herb. Boissier, ser. 2, 8: 635. 1908. TYPE: *Pseudotragia scandens* Pax [= *Plukenetia africana* Sond.].

Eleutherostigma Pax & K.Hoffm. in A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 11, t.3. 1919. TYPE: *Eleutherostigma lehmanniana* Pax & K.Hoffm. [= *Plukenetia lehmanniana* (Pax & K.Hoffm.) Huft & L.J.Gillespie].

Angostylidium (Müll.Arg.) Pax & K.Hoffm. in A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 17. 1919. *Plukenetia* sect. *Angostylidium* Müll.Arg., Flora 47: 530. 1864. TYPE: *Angostylidium conophorum* (Müll.Arg.) Pax & K.Hoffm. [= *Plukenetia conophora* Müll.Arg.].

Apodandra Pax & K.Hoffm. in A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 20. 1919. TYPE (lectotype designated by Webster 1994): *Apodandra lorentensis* (Ule) Pax & K.Hoffm. [= *Plukenetia lorentensis* Ule].

Elaeophora Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 112. 1925. TYPE: *Elaeophora abutifolia* Ducke [= *Plukenetia polyadenia* Müll.Arg.].

Notes—See Gillespie (2007) for genus description.

KEY TO THE SECTIONS OF *PLUKENETIA*

1. Leaf venation pinnate, primary vein 1 (palmate, primary veins 3 in *P. verrucosa*); styles entirely connate into a cylindrical, depressed-subglobose, globose, obovoid, or oblong-obovoid column, 0.3–4.5 mm long; pollen tecta coarsely reticulate. 2 (Pinnately veined clade, subclades P1 + P2)
2. Fruits 4–5 cm in diam, fleshy; pistillate flowers 1–10 per inflorescence; all anthers sessile and loosely packed on a globose receptacle, receptacles 2 mm or more in diam, visible between anthers; stipels 2, present adaxially at petiole apex; distributed in the Atlantic Forest region of Brazil. II. P. sect. *Fragariopsis*
2. Fruits 0.9–1.5 cm in diam, dry; pistillate flowers 1 per inflorescence; all or most anthers sessile and densely packed on a globose or subglobose receptacle, receptacles less than 1 mm in diam, not visible between anthers; stipels absent adaxially at petiole apex (2 in *P. verrucosa*); distributed in Mexico, Central America, northwestern and Amazonian South America, and the Lesser Antilles. V. P. sect. *Penninerviae*
1. Leaf venation palmate, primary veins 3(–5); styles partly connate into a cylindrical column, 1–35 mm long (entirely connate into a depressed-globose column 0.5–0.7 mm long in *P. corniculata*, or an obconic or obovoid column 3.5–5.5 mm long in *P. ankaranensis*); pollen tecta foveolate. 3 (Palmately veined clade, subclades P3–P5)
3. Styles 0.5–1.7 mm long, shorter than or nearly equal in length to the ovary; fruits dry capsules, 1.1–2 cm in diam; distributed in southern Africa or Southeast Asia. III. P. sect. *Hedraiostylus*
3. Styles 3.5–35 mm long, longer than the length of the ovary; fruits dry capsules or fleshy berries, 2.3–11 cm in diam; distributed in tropical central and western Africa, Madagascar, or the Neotropics. 4
4. Staminate receptacles ellipsoid, oblong-cylindrical, or ovoid-conical; anthers sessile; nectaries absent; distributed in Madagascar. IV. P. sect. *Madagascarienses*
4. Staminate receptacles convex to subglobose; anthers on short-conical or slender-cylindrical filaments, 0.5–3 mm long; nectaries of interstaminal slender-cylindrical, ligulate, or small or large irregularly shaped segments (absent in *P. volubilis*); distributed in tropical central and western Africa or the Neotropics. 5
5. Stylar columns funnel-shaped, free style arms conspicuously dilated and spreading; stipels and glandular knobs absent adaxially at petiole apex; distributed in tropical central and western Africa. I. 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; distributed in the Neotropics. VI. P. sect. *Plukenetia*

1. *PLUKENETIA* sect. *ANGOSTYLIDIUM* Müll.Arg., *Flora* 47: 530. 1864. *Angostylidium* (Müll.Arg.) Pax & K.Hoffm. in A.Engler (ed.), *Pflanzenr.* IV, 147, IX (Heft 68): 17. 1919. TYPE: *Plukenetia conophora* Müll.Arg.

Canopy lianas, stems thick. **Leaf venation** palmate, primary veins 3. **Inflorescences** unisexual or functionally unisexual; staminate inflorescences racemose thyrses, staminate flowers 3–7/ node in condensed cymules, sometimes with 1–2 apparently non-functional pistillate flowers at basal-most nodes; pistillate inflorescences short racemes, pistillate flowers solitary at 1–2(3) basal-most nodes, axes mostly aborted above (rarely with a few staminate flowers in cymules). **Staminate flowers:** receptacle subglobose; nectaries numerous interstaminal slender-cylindrical segments; stamens 25–50, densely packed; filaments conical, < 0.5 mm long; pollen P = 34–38 μm , E = 41–46 μm , tectum foveolate. **Pistillate flowers:** styles 75(–90)% connate into a funnel-shaped column, entire style 4–7.5 mm long. **Fruits** 4(5)-lobed or subglobose-quadrangular, capsule-like, fleshy, indehiscent, 4.5–7.5 cm in diam. **Seeds** broadly ovoid or subglobose, 25–29 \times 25–27 \times 25–28 mm (“extra-large” sensu Cardinal-McTeague et al. 2019a).

The single species in this section is distributed in tropical central and western Africa.

Discussion—Section *Angostylidium* corresponds to subclade P4 (Fig. 1) and includes a single species, *P. conophora*, from tropical central and western Africa. This Old World species/section is morphologically similar to sect. *Plukenetia* of the Neotropics. Both sections have staminate flowers with interstaminal nectaries (absent in *P. volubilis* of sect. *Plukenetia*), partly connate styles, often larger fleshy fruits (although dry fruits are just as frequent in sect. *Plukenetia*), and often larger seeds (usually “large” and “extra-large”). Phylogenetic relationships suggest these characters are symplesiomorphic for the palmately veined clade (P3–P5). Section *Angostylidium* is differentiated by its African moist to wet tropical distribution, functionally unisexual inflorescences, and funnel-shaped stylar column with conspicuously dilated and spreading free style arms (Fig. 3L).

1. *PLUKENETIA* *CONOPHORA* Müll.Arg., *Flora* 47: 530. 1864. *Angostylidium conophorum* (Müll.Arg.) Pax & K.Hoffm. in

A.Engler (ed.), *Pflanzenr.* IV, 147, IX (Heft 68): 17. 1919. *Cleidion mannii* Baker, *Bull. Misc. Inform. Kew* 1910 (2): 58. 1910, nom. illeg. *Tetracarpidium conophorum* (Müll.Arg.) Hutch. & Dalziel, *Fl. W. Trop. Afr.* 1: 307. 1928. TYPE: CAMEROON. River Cameroon, January 1863, G. Mann 2202 (lectotype designated by Gillespie 2007: K! [barcode K000425658]; isolectotypes: K! [barcode K000425659], K! [barcode K000425660]).

Mallotus preussii Pax, *Bot. Jahrb. Syst.* 23 (4): 525. 1897. *Cleidion preussii* (Pax) Baker, *Bull. Misc. Inform. Kew* 1910 (9): 343. 1910. TYPE: CAMEROON. Barombistation, 25 August 1890, P.R. Preuss 420 (holotype: B [destroyed]; lectotype designated here: K! [barcode K000252567]; isolectotype: BM! [barcode 000535904 (BM)]).

Tetracarpidium staudtii Pax, *Bot. Jahrb. Syst.* 26 (3–4): 329. 1899. TYPE: CAMEROON. Station Johann-Albrechtschöhe, 15 January 1897, A. Staudt 802 (holotype: B [destroyed]; lectotype designated here: BM! [barcode 000535187 (BM)]; isolectotypes: G [barcode G00414564; image!], K! [barcode K000425656; sketch of holotype with floral fragments], MO! [accession 1648824, barcode MO-2289110], PH [accession 01078710, barcode 00030257; image!]).

Notes—See Gillespie (2007) for species description.

Taxonomic Discussion—*Plukenetia conophora* and sect. *Angostylidium* were simultaneously described by Müller (1864). Subsequent authors described taxa that are now treated as synonyms, including *Mallotus preussii* (Pax 1897) and the novel genus and species *Tetracarpidium staudtii* (Pax 1899). Furthermore, Baker (1910) described *Cleidion mannii* from *P. conophora* syntype material (“River Cameroon.” G. Mann 2202) but erroneously cited the type as “Cameroons river, G. Mann 1202” (that specimen is recorded as *Pittosporum viridiflorum* “mannii” Sims, “Mount Cameroon,” G. Mann 1202 (K000106232). Baker appears to have described *Cleidion mannii* from the only G. Mann 2202 sheet at Kew that was not annotated as Müller’s *P. conophora* (K000425659).

The holotype of *Mallotus preussii* is presumed to have been in Berlin, where Pax worked and Preuss’s main collections were housed. Since the type was likely destroyed, we designate a

lectotype from an isotype housed at Kew, given it has abundant staminate flowers. Under a similar circumstance we designate a lectotype for *Tetracarpidium staudtii*, selecting the isotype with the most abundant leaf and pistillate flower material housed at the British Museum. Alois Staudt was the collection assistant of G. Zenker in Cameroon, so we presume his collections were part of Zenker's main set that was destroyed in Berlin.

II. *Plukenetia* sect. *Fragariopsis* (A.St.-Hil.) Card.-McTeag. & L.J.Gillespie, comb. et stat. nov. *Fragariopsis* A.St.-Hil., *Leçons Bot.* 426. 1840. TYPE: *Fragariopsis scandens* A.St.-Hil. [= *Plukenetia serrata* (Vell.) L.J.Gillespie]

Lianas, stems slender to thick. **Leaf venation** pinnate, primary vein 1. **Inflorescences** bisexual racemose thyrses; pistillate flowers solitary at 1–10 basal-most nodes; staminate flowers 2(3)/node in condensed cymes. **Staminate flowers:** receptacle globose; nectaries absent; stamens 10(–20), loosely packed (receptacle clearly visible between anthers); filaments absent; pollen $P = 32\text{--}46\ \mu\text{m}$, $E = 42\text{--}55\ \mu\text{m}$, tectum coarsely reticulate. **Pistillate flowers:** styles entirely connate into an obovoid column, 3–3.5 mm long. **Fruits** 4-lobed or subglobose-quadrangular, capsule-like, initially fleshy, apparently indehiscent or tardily splitting, 4–5 cm in diam. **Seeds** subglobose, 15–15.5 × 15.5–16 × 15–16 mm (“large” sensu Cardinal-McTeague et al. 2019a).

The single species in this section is distributed in the Atlantic Forest of Brazil.

Etymology—The sectional epithet is derived from *Fragaria* (Latin, strawberry) and *-opsis* (Greek, appearing like or resembling), referring to the androecium, which has the appearance of a small strawberry. We chose the name *Fragariopsis* because it describes the androecium morphology that is unique to the section and because historically it was the more widely known genus that contained *Plukenetia serrata*.

Discussion—Section *Fragariopsis* refers to subclade P1 (Fig. 1) and includes a single species, *P. serrata*, from the Atlantic Forest region of Brazil. This species/section has long been recognized as a distinct genus (Table 1), but belongs within *Plukenetia* due to their numerous shared characters (Gillespie 1993) and phylogenetic relationships (Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019a). Together, sects. *Fragariopsis* and *Penminerviae* constitute the pinnately veined clade (P1 + P2), which is united by pinnate leaf venation, coarsely reticulate pollen tecta, all or mostly sessile anthers, and entirely connate styles. Section *Fragariopsis* is differentiated by its unique androecium composed of sessile anthers loosely packed on a globose receptacle (Fig. 2B), as well as by having 1–10 pistillate flowers, “large” seeds derived from fleshy fruits, and for being the only section distributed in the Atlantic Forest region of Brazil.

2. *PLUKENETIA SERRATA* (Vell.) L.J.Gillespie, *Syst. Bot.* 18 (4): 587. 1993. *Vigia serrata* Vell., *Fl. Flumin. Icon.* 9: t.128. 1827 publ. 29 October 1831. TYPE: BRAZIL. Illustration t.128 in Vellozo, *Fl. Flumin. Icon.* 9. 1827 publ. 29 October 1831.

Fragariopsis scandens A.St.-Hil., *Leçons Bot.* 426. 1840. *Plukenetia scandens* (A.St.-Hil.) Pax in Engler & Prantl (eds.), *Nat. Pflanzenfam.* 3 (5): 67. 1890. TYPE: BRAZIL. 1816–1821. *A. de Sainte-Hilaire* 95 (lectotype designated here: P! [barcode P00072051]; isolectotype: P! [barcode P00072052]).

Accia scandens A.St.-Hil., *Leçons Bot.* 499. 1840, nom. illeg. TYPE: not designated. [Likely based on the same syntypes

as *Fragariopsis scandens*, therefore a nomenclatural synonym and an illegitimate name; one of the syntype collections, *A. de Saint-Hilaire* D 72 (barcodes P00072053!, P00072054!), is annotated as both *Accia* and *Fragariopsis scandens*, but the first name appears to be a later addition.]

Botryanthe discolor Klotzsch, *Arch. Naturgesch.* (Berlin) 7 (1): 191, 204. Table 9b. 1841. *Fragariopsis discolor* (Klotzsch) Baill., *Étude Euphorb.* 498. 1858. TYPE: BRAZIL. *F. Sellow s.n.* (holotype: B [destroyed]; lectotype designated by Gillespie 1993: P! [barcode P00072049]; isolectotypes: F! [fragment], HBG [barcode HBG-516131; image!]). [Klotzsch's species *Botryanthe concolor* given in the same publication was not validly published.]

Fragariopsis polyandrus Baill., *Étude Euphorb.* 498. 1858. *Fragariopsis scandens* var. *polyandrus* (Baill.) Baill., *Adansonia* 5: 318. 1865. TYPE: BRAZIL. Rio de Janeiro, Mont. Corcovado, Sainte-Thérèse, May 1839, J.B.A. *Guillemin cat. n.* 798 (lectotype designated here: P! [barcode P00072048]; isolectotypes: G-DC! [pro parte, left specimen excluding packets; barcode G00313646], P! [barcode P00072047], P [as J.-B. *Houillet cat. n.* 798; barcode P05564458; image!]).

Fragariopsis warmingii Müll.Arg. in Martius (ed.), *Fl. Bras.* 11 (2): 338. 1874. *Plukenetia warmingii* (Müll.Arg.) Pax in Engler & Prantl (eds.), *Nat. Pflanzenfam.* 3 (5): 67. 1890. TYPE: BRAZIL. Minas Gerais: Lagoa Santa, *E. Warming s.n.* (holotype: P! [barcode P00072055]; isotype: F! [fragment]; probable isotype: F!).

Notes—See Gillespie (1993) for species discussion.

Taxonomic Discussion—*Plukenetia serrata* was first described as *Vigia serrata* (Vellozo 1831) but was widely known as *Fragariopsis scandens* (Saint-Hilaire 1840) until the priority of Vellozo's name was identified by Gillespie (1993). In the same publication, Saint-Hilaire (1840) described *Accia scandens*, which is likely a superfluous name for *F. scandens* based on the same syntypes. The description of *Fragariopsis* only includes the staminate flowers, whereas *Accia* is only of the pistillate flowers, however both descriptions are indicative of *P. serrata*. *Botryanthe* was independently described by Klotzsch (1841) and was synonymized along with *Accia* under *Fragariopsis* by Baillon (1858). Two additional species, *F. polyandrus* (Baillon 1858) and *F. warmingii* (Müller 1874), were described, but both are treated as synonyms of *P. serrata* (Gillespie 1993). However, phylogenetic data indicates there is substantial nucleotide variation within *P. serrata* (Cardinal-McTeague et al. 2019a), suggesting its species boundaries should be reassessed with better taxon sampling across its morphological and geographical ranges.

Saint-Hilaire (1840) did not cite a collection number in his original species description of *Fragariopsis scandens*, but two of his collections, each with a duplicate, are housed at P. All four sheets have sufficient vegetative and floral material to identify the species; however, to clarify the type status we designate the best sheet (*A. de Saint-Hilaire* 95; P00072051) as lectotype. Remaining syntype: BRAZIL. Minas Gerais, 1816–1821, *A. de Saint-Hilaire* D 72 (P! [barcodes P00072053, P00072054]).

Fragariopsis polyandrus has a complicated type history. Baillon (1858) did not cite any types for *F. polyandrus* but indicated its species illustrations in Tab. XIII were based on material from “Herb. Houillet” (Atlas, p. 26). Baillon (1865) later cited a single specimen with *F. scandens* var. *polyandrus*, “*Guillemin et Houillet* (herb.), cat., n. 798”, which matches J.B.A. *Guillemin cat. n.* 798

specimens housed at P and G-DC. To complicate matters, another collection of *Fragariopsis scandens* was found at Paris, J.-B. Houillet cat. n. 798. Notably, the Houillet collection includes the locality information cited by Baillon (1865), which is missing from the J.B.A. Guillemain cat. n. 798 sheets at P and G-DC. Guillemain and Houillet were collecting partners in Brazil and many of Guillemain's collections appear to have been brought to Paris by Houillet, who later worked as the Jardinier en chef des Serres. Since the Guillemain and Houillet collections are of the same species, share the same catalogue number, and are associated together by Baillon (1865), we consider them the same collection. We designate a lectotype for *F. polyandrus* based on the P specimen with the most abundant pistillate flowers (note that all of these specimens have dropped and lost their staminate flowers, and that the staminate flowers in the packets of the G-DC sheet appear to belong to the other collection of *F. scandens* sharing the sheet).

III. PLUKENETIA sect. HEDRAIOSTYLUS (Hassk.) Müll.Arg., D.C. Prod. 15 (2): 772. 1866. *Hedraiostylus* Hassk., Tijdschr. Natuurl. Gesch. Physiol. 10: 141. 1843. *Sajorium* sect. *Hedraiostylus* (Hassk.) Baill., Étude Euphorb. 483. 1858. TYPE: *Hedraiostylus glaberrimus* Hassk. [= *Plukenetia corniculata* Sm.]

Plukenetia sect. *Sajor* Müll.Arg., Linnaea 34: 159. 1865. TYPE: not designated.

Plukenetia sect. *Pterococcus* (Hassk.) Benth. & Hook., Gen. Pl. 3, 1: 327. 1880. *Pterococcus* Hassk., Flora 25 (2, Bleibl.): 41. 1842, nom. cons., non. Pall. 1773. TYPE: *Pterococcus glaberrimus* (Hassk.) Hassk. [= *Plukenetia corniculata* Sm.]

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

1. Petioles > (1–)3 cm long; leaf blades > (2–)4 cm wide, base deeply cordate, stipels present adaxially at petiole apex ~0.5–1 mm long; capsules with strap-shaped wing 6–12 mm long on each carpel lobe; distributed in Southeast Asia 4. *P. corniculata*
1. Petioles < 1 cm long; leaf blades < 3.5 cm wide, base obtuse to truncate, hastate, or rarely sagittate, stipels present adaxially at petiole apex, 0.1–0.6 mm long, or absent; capsules with tubercle or wing ≤ 3 mm long on each carpel lobe; distributed in southern Africa. 2
2. Leaf blades narrowly triangular, lanceolate, or linear-lanceolate, 3–8 cm long, base often hastate; adaxial basilaminar extrafloral nectaries (0–)2, 0.2–0.3 mm in diam 3. *P. africana*
2. Leaf blades elliptic or ovate, 2–4.5 cm long, base obtuse to rounded; adaxial basilaminar extrafloral nectaries 2–12(–20), 0.2–0.8 mm in diam 5. *P. procumbens*

3. PLUKENETIA AFRICANA Sond., Linnaea 23: 110. 1850. *Pterococcus africanus* (Sond.) Pax & K.Hoffm. in A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 22. 1919. TYPE: SOUTH AFRICA. Magalisberg, auf Grasfeldern, October, C.L.P. Zeyher 1522 (holotype: S! [accession S-G-10556]; isotypes: BM!, G! [barcode G00441997], K! [barcode K000425662], MEL [barcode MEL501283; fragment; image!]).

Plukenetia hastata Müll.Arg., Flora 47: 469. 1864. TYPE: MOZAMBIQUE. Between Shupanga & Senna, Portuguese East Africa, on the Lower Zambesi, 14°–19° S, January 1859, J. Kirk s.n. (holotype: K! [barcode K000425661]).

Pseudotragia schinzii Pax, Bull. Herb. Boissier, ser. 2, 8: 635. 1908. TYPE: NAMIBIA. Amboland, Otjiheveta, 1886, H. Schinz 895 (holotype: G; isotypes: K! [barcode K001044972], Z [barcode Z-000085917; image!]).

Pseudotragia scandens Pax, Bull. Herb. Boissier, ser. 2, 8: 636. 1908. TYPE: NAMIBIA. Amboland, Oohama, March 1886, H. Schinz 894 (holotype: G; isotypes: K! [barcode K001044973], Z [barcode Z-000085918; image!]).

Notes—See Gillespie (2007) for species description.

Although Sonder did not explicitly cite holotypes, his types based on Ecklon and Zeyher collections from South Africa are

Vines, lianas, or perennial herbs, stems slender, twining or sometimes procumbent. **Leaf venation** palmate, primary veins 3(–5). **Inflorescences** bisexual racemes (rarely racemose thyrses); pistillate flowers solitary (rarely 2) at basal-most node(s); staminate flowers 1/node (sometimes 1–2/node in reduced condensed cymules). **Staminate flowers**: receptacle convex, subglobose, or globose; nectaries absent; stamens 8–20, densely packed; filaments conical, < 0.5 mm long; pollen P = 34–40 μm, E = 40–50 μm, tectum foveolate. **Pistillate flowers**: styles entirely connate into a depressed-globose or stout-cylindrical column, 0.5–1.4 mm long, or ~70% connate into a stout-cylindrical column with spreading free style arms, 1.3–1.7 mm long. **Fruits** 4-lobed capsules, dry, dehiscent, 1.1–2 cm in diam. **Seeds** broadly lenticular, 5.5–10.5 × 5–8 × 2.5–8 mm (“small” or “medium” sensu Cardinal-McTeague et al. 2019a).

The species in this section are distributed in southern Africa and Southeast Asia.

Discussion—Section *Hedraiostylus* refers to a strongly supported clade within subclade P5 (Fig. 1) and includes three species, *P. africana* and *P. procumbens* from southern Africa and *P. corniculata* from Southeast Asia. This section is weakly defined morphologically but appears to be united by short styles < 2 mm long, usually shorter than the length of the ovary (although slightly longer than the ovary in *P. procumbens*), staminate flowers with short-conical filaments and lacking nectaries, smaller dry dehiscent fruits, and “small” or “medium” seeds. The southern African species are unique for growing in seasonally dry wooded savannas and have evolved thick rootstocks that facilitate resprouting after fires.

presumed to be housed in S (Nordenstam 1980), with duplicates found in many other herbaria in Europe and Melbourne, Australia. Indeed, the specimen at Stockholm, which we consider the holotype, has the most abundant floral and fruit material and original labels.

4. PLUKENETIA CORNICULATA Sm., Nova Acta Regiae Soc. Sci. Upsal. 6: 4. 1799. *Pterococcus glaberrimus* Hassk., Flora 25 (2): 41. 1842. *Hedraiostylus glaberrimus* (Hassk.) Hassk., Tijdschr. Natuurl. Gesch. Physiol. 10: 141. 1843. *Hedraiostylus corniculatus* (Sm.) Hassk., Cat. Hort. Bot. Bogor. 234. 1844. *Sajorium corniculatum* (Sm.) D.Dietr., Syn. Pl. 5: 331. 1852. *Sajorium corniculatum* (Sm.) Baill., Étude Euphorb. 484. 1858, nom. illeg. *Pterococcus corniculatus* (Sm.) Pax & K.Hoffm. in A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 22. 1919. TYPE: INDONESIA. Amboina, Bagulae Regione, Illustration t.79, Fig. 2 in Rumphius, Herb. Amboin. 1: 193. 1750.

Notes—See Gillespie (2007) for species description.

Taxonomic Discussion—*Plukenetia corniculata* is one of the oldest names in *Plukenetia* and has a complicated taxonomic history. Originally described as the pre-Linnaean *Sajor volubilis* (Rumphius 1750), it was included as a synonym of *Plukenetia volubilis* by Linnaeus (1753). Smith (1799) gave Rumphius'

species its first legitimate name, *P. corniculata*, but four other genera would be erected for *Sajor*: *Pterococcus* (Hasskarl 1842), *Hedraiostylus* (Hasskarl 1843), *Sajorium* (Endlicher 1843), and *Ceratococcus* (Meisner 1843). Hasskarl's first name, *Pterococcus* (1842), was previously published by Pallas (1773) in Polygonoaceae, so he proposed the replacement name *Hedraiostylus* in ~September 1843 (Stafleu and Cowan 1979). Subsequent replacement names *Sajorium* and *Ceratococcus*, both nomenclaturally superfluous, were published in October and 2–4 November of 1843, respectively (Stafleu and Cowan 1976, 1981).

Baillon (1858) first treated *Hedraiostylus* as a section of the illegitimate genus *Sajorium* [= *Plukenetia*], giving *Hedraiostylus* priority as a sectional name. The fact that *Sajorium* was illegitimate precludes the rejection of sect. *Hedraiostylus* in favour of the autonym *Sajorium* sect. *Sajorium* (ICN 2017, Art. 22.5; Turland et al. 2018). When Müller created the first sectional classification of *Plukenetia* he initially erected sect. *Sajor* (Müller 1865), but quickly updated it to sect. *Hedraiostylus* (Müller 1866). To complicate matters, *Pterococcus* Hassk. was conserved over *Pterococcus* Pall., but as a sectional name, *Hedraiostylus* retains priority.

5. PLUKENETIA PROCUMBENS Prain, Bull. Misc. Inform. Kew 1912 (5): 240. 1912. *Pterococcus procumbens* (Prain) Pax & K.Hoffm. in A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 23. 1919. TYPE: ANGOLA. Benhuella, Ganguella, on the Cubagano River at Princeza Amelia, 1520 m, 27 January 1907, J. Gossweiler 2540 (holotype: BM! [barcode 000535903 (BM)]; isotypes: COI! [barcode COI00072615], K! [barcode K000425657; fragments with floral sketch]).

Notes—See Gillespie (2007) for species description.

- IV. *Plukenetia* sect. *Madagascarienses* Card.-McTeag. & L.J.Gillespie sect. nov. TYPE: *Plukenetia madagascariensis* Leandri.

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

1. Styles entirely connate, 3.5–5.5 mm long, styler column obconic or obovoid, free style arms absent; androecia 0.6–1 mm long, anthers 15–20; inflorescences thyrses, terminal and appearing leaf-opposed, staminate flowers in distinct cymules; glandular knobs absent at petiole apex. 6. *P. ankaranensis*
1. Styles 55–60% connate, entire style 8–16 mm long, styler column cylindrical, free style arms slender, tapered; 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
 2. 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 oblong-ellipsoid receptacle; leaf blades triangular-ovate or ovate. 7. *P. decidua*
 2. 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. 8. *P. madagascariensis*

6. PLUKENETIA ANKARANENSIS L.J.Gillespie, Syst. Bot. 32 (4): 797. 2007. TYPE: MADAGASCAR. Antsiranana Province: Special Reserve #3, Ankarana, ca. 7 km SE of Matsaborimanga, trail between Camp Anglais and river (ca. 3 km SW Camp Anglais), [-12.917°, 49.1°], 150 m, 28 November 1990, L.J. Gillespie 4076 (holotype: MO! [accession 6128360, barcode MO-2246124]; isotypes: CAN! [accession 589544], DAV! [accession 182695, barcode DAV 182695], G! [barcode G00386814], K! [barcode K001044974], L!, NY! [barcode 01104761], P! [barcode P00717080], TAN!, US!; FAA preserved material at MO).

Notes—See Gillespie (2007) for species description.

7. PLUKENETIA DECIDUA L.J.Gillespie, Syst. Bot. 32 (4): 798. 2007. TYPE: MADAGASCAR. Sud-Ouest, entre Ampanihy et Itrobiky (route Ampanihy-Androka), 4 July 1958, R. Capuron

Lianas, stems slender to thick. **Leaf venation** palmate, primary veins 3(–5). **Inflorescences** bisexual racemes or racemose thyrses; pistillate flowers solitary at 1–2 basal-most nodes; staminate flowers 1/node or 3–5/node in lax or moderately condensed cymules with conspicuous and irregularly branched cyme axes. **Staminate flowers**: receptacle ellipsoid, oblong-cylindrical, or ovoid-conical; nectaries absent; stamens 15–60, densely or loosely packed; filaments absent; pollen P = 28–41 μm, E = 35–51 μm, tectum foveolate. **Pistillate flowers**: styles entirely connate into an obconic or obovoid column, 3.5–5.5 mm long, or 55–60% connate into a cylindrical column, 8–16 mm long, free style arms slender and tapered. **Fruits** 4-lobed capsules, dry, dehiscent, 2.3–4 cm in diam. **Seeds** broadly ellipsoid or subglobose, 13.1–18 × 11.1–17 × 11.2–17 mm (“large” sensu Cardinal-McTeague et al. 2019a).

The species in this section are distributed in Madagascar.

Etymology—The sectional epithet is derived from the combination of Madagascar and *-ensis* (Latin, of a place), which reflects that all the species in the section are endemic to Madagascar.

Discussion—Section *Madagascarienses* refers to a strongly supported clade within subclade P5 (Fig. 1) and includes three species endemic to Madagascar. This section was originally defined as the Madagascan species group (Gillespie 2007) and was noted for exhibiting sessile anthers similar to the pinnately veined clade. Style morphology is variable in the section, including both partly (*P. decidua*, *P. madagascariensis*) and entirely connate (*P. ankaranensis*) styles (Fig. 3N–O). Section *Madagascarienses* is differentiated by having sessile anthers on a prominently elongated receptacle (Fig. 2L), larger dry dehiscent fruits, “large” seeds, and by being endemic to Madagascar. All three species occur in seasonally dry environments, either dry forest on tsingy limestone (*P. ankaranensis*, *P. madagascariensis*) or in dry scrub (*P. decidua*).

18682-SF (holotype: P! [barcode P00586758]; isotypes: P! [barcode P00586759], P! [barcode P00586760]).

Notes—See Gillespie (2007) for species description.

8. PLUKENETIA MADAGASCARIENSIS Leandri, Bull. Bot. Soc. France 85: 527. 1938 publ. 1939. TYPE: MADAGASCAR. Mahajanga: Bois à Morataitra, rive droite de Betsiboka, est de Mae-vatanana (Boeny), March 1899, H. Perrier 848 (lectotype designated by Gillespie 2007: P! [barcode P00586763]; isolectotypes: L! [accession 301470, barcode L 0388568], P! [barcode P00586764], P! [barcode P00586765]).

Notes—See Gillespie (2007) for species description.

V. *Plukenetia* sect. *Penninerviae* Card.-McTeag. & L.J. Gillespie
sect. nov. TYPE: *Plukenetia penninervia* Müll.Arg.

Vines or lianas, stems slender. **Leaf venation** pinnate, primary vein 1 (palmate, primary veins 3 in *P. verrucosa*). **Inflorescences** bisexual racemose thyrses (racemes in *P. brachybotrya*); pistillate flowers solitary at basal-most node; staminate flowers 1–3(–5)/node in condensed cymules, sometimes appearing short racemose, or 1/node. **Staminate flowers:** receptacle globose or subglobose; nectaries absent or an extrastaminal annular ring (3–6-lobed, or unlobed with an uneven or undulate upper surface); stamens 6–50, anthers sessile and densely packed on the receptacle, sometimes with an outer whorl of 3–4 filamentous stamens; filaments absent or slender-cylindrical 0.2–1 mm long in outer whorl; pollen P = 31–62 µm, E = 39–76 µm, tectum coarsely reticulate. **Pistillate flowers:** styles entirely connate into a depressed-subglobose, globose, obovoid, oblong-obovoid, stout-cylindrical, or slender-cylindrical column with a dilated apex, 0.3–4.5 mm long. **Fruits** 4-lobed capsules, dry, dehiscent, 0.9–1.5 cm in diam. **Seeds** globose, subglobose, or broadly lenticular, 4.5–7.3 × 3.7–7.1 × 3–5.2 mm, (“small” or “medium” sensu Cardinal-McTeague et al. 2019a).

The species in this section are distributed in Mexico, Central America, northwestern and Amazonian South America, and the Lesser Antilles.

Etymology—The sectional epithet is derived from *penni-* (Latin, feather) and *-nervia* (Latin, -nerved or -veined), referring to the pinnately veined leaves exhibited by most species in the section (excluding *P. verrucosa*).

Discussion—Section *Penninerviae* refers to subclade P2 (Fig. 1) and includes nine species distributed throughout the Neotropics. This section was erroneously referred to as sect. *Euplukenetia* by Pax and Hoffmann (1919), but that name was both invalid and incorrectly attributed to a section excluding the type species, *P. volubilis*. Section *Penninerviae* forms a major component of the pinnately veined clade (P1 + P2), and is distinguished by having staminate flowers with sessile anthers densely packed on a globose receptacle (Fig. 2C), frequently with an extrastaminal annular or segmented nectary (see *P. brevistyla* and *P. megastyla*) and/or an outer whorl of 3–4 filamentous stamens (Fig. 2D–E). It differs from sect. *Fragariopsis* by having a single pistillate flower per inflorescence and “small” seeds borne in small dry dehiscent capsules.

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

1. Leaf venation palmate, primary veins 3, base subcordate to truncate; stipels 2, present adaxially at petiole apex; stylar column globose, subglobose, or obovoid. 17. *P. verrucosa*
1. Leaf venation pinnate, primary vein 1, base rounded to attenuate; stipels absent adaxially at petiole apex; stylar column slender-cylindrical, stout-cylindrical, depressed-subglobose, globose, or oblong-obovoid. 2
2. Adaxial basilaminar extrafloral nectaries 1 pair; stylar columns depressed-subglobose, globose, or oblong-obovoid. 3
3. Stylar columns globose; stamens: 30–50 sessile anthers; staminate nectaries absent. 9. *P. brachybotrya*
3. Stylar columns depressed-subglobose or oblong-obovoid; stamens: 16–30 sessile anthers, sometimes ~3 basal-most stamens on short filaments; staminate nectaries an annular ring with an uneven or undulate upper surface, sometimes 3-segmented or absent. 4
4. Stylar columns depressed-subglobose, 0.3–1 mm long; staminate sepals 3, often recurved at anthesis; stamens 16–20 usually sessile anthers, sometimes ~3 basal-most stamens with short filaments; petioles generally of uniform thickness and colour; fruit carpels usually unornamented, sometimes with a short tubercle. 10. *P. brevistyla*
4. Stylar columns oblong-obovoid, 2.6–4.4 mm long; staminate sepals 3–4, incurved to spreading at anthesis; stamens 20–30 sessile anthers; petioles with thickened, often purplish pulvinus-like regions at base and apex; fruit carpels usually with a short tubercle, sometimes unornamented. 13. *P. megastyla*
2. Adaxial basilaminar extrafloral nectaries 1–5 pairs; stylar columns slender-cylindrical, stout-cylindrical, or obovoid-cylindrical. 5
5. Stylar columns slender-cylindrical, 2.5–4.8 mm long; stamens of one type: 15–25 sessile anthers on a globose receptacle; staminate nectaries absent. 12. *P. lorensis*
5. Stylar columns stout- or obovoid-cylindrical, 0.9–2(3) mm long; stamens of two types: 6–15 sessile anthers on a globose receptacle and an outer whorl of 3–4 stamens with filaments; staminate nectaries annular, 3–6-lobed or absent. 6
6. Adaxial basilaminar extrafloral nectaries 3–5 pairs; young shoots and petioles densely hirsute; leaf blades hirsute abaxially. 14. *P. multiglandulosa*
6. Adaxial basilaminar extrafloral nectaries 1–2(3) pairs; young shoots and petioles puberulent; leaf blades glabrous to sparsely puberulous abaxially. 7
7. Scattered laminar extrafloral nectaries numerous, present on both leaf surfaces; leaf blades chartaceous, margins minutely serrulate, appearing undulate, never distinctly glandular; inflorescences 2–8 cm long. 16. *P. supraglandulosa*
7. Scattered laminar extrafloral nectaries absent or 1–8 near margin on abaxial leaf surface; leaf blades thick-chartaceous to coriaceous, margins distinctly serrulate, often distinctly glandular (*P. penninervia*); inflorescences 0.5–3 cm long (to 6 cm long in late staminate stage of *P. chocoensis*). 8
8. Adaxial basilaminar extrafloral nectaries narrowly oblong-elliptic, base short attenuate and clasping; abaxial laminar extrafloral nectaries 1–8 near the margin; staminate stage inflorescences 1.5–6 cm long; leaf blades drying olive-green with darker orange-brown abaxial venation. 11. *P. chocoensis*
8. Adaxial basilaminar extrafloral nectaries small and circular, base obtuse or rounded and non-clasping; abaxial laminar extrafloral nectaries usually absent; staminate stage inflorescences 1–2 cm long; leaf blades drying grey-green with pale-cream or straw-coloured abaxial venation. 15. *P. penninervia*

9. *PLUKENETIA BRACHYBOTRYA* Müll.Arg., Linnaea 34: 158. 1865.
Apodandra brachybotrya (Müll.Arg.) J.F.Macbr., Publ. Field
Columb. Mus., Bot. Ser., 13 (3a, 1): 117. 1951. TYPE: PERU.
Peruvia, “Herb. Pavon” [likely *H. Ruiz & J. Pavón s.n.*]
(holotype: G-BOIS! [barcode G00441995]; isotypes: G!
[barcode G00441996], G-DC! [barcode G00313654]).

1907, O. Buchtien 1962 (lectotype designated by Gillespie
1993: US! [accession 1175161, barcode 00096450]; iso-
lectotypes: NY! [barcode 00273178], Z [barcode Z-
000019739; image!]).

Notes—See Gillespie (1993) for species discussion.

Müller cited the protologue of *P. brachybotrya* as “hb. Pavon!
in hb. Boiss.” suggesting the holotype was a Pavon collection
housed in Boissier’s herbarium. Given that there is only one
such sheet in Boissier’s herbarium (now housed at G), we
maintain that it is a holotype and not in need of lectotypification.

Plukenetia buchtienii Pax, Repert. Spec. Nov. Regni Veg. 7: 110.
1909. *Apodandra buchtienii* (Pax) Pax & K.Hoffm. in
A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 21. 1919.
TYPE: BOLIVIA. Charopompa bei Mapiri, 570 m, November

10. *Plukenetia brevistyla* Card.-McTeag. & L.J.Gillespie sp. nov. TYPE: BRAZIL. Amazonas, km 320 on Manaus-Humaitá road, 16 September 1980, S.R. Lowrie, B. Lowy, D. Coelho, M. Morreira & V.M. de Souza 30 (holotype: MO! [accession 2926690, barcode MO-1381795]; isotypes: CAN!, NY!, RB [accession 564286, barcode RB00749078, image!], US!).

Similar to *P. brachybotrya* Müll.Arg. and *P. megastyla* Card.-McTeag. & L.J.Gillespie, but with a short depressed-subglobose stylar column, 0.3–1 mm long.

Monoecious slender lianas; stems erect or twining; older stems dull light grey-brown or straw-coloured, to ~5 mm in diam, striate or weakly striate, glabrate with patches of exfoliating cuticle; younger stems smooth to striate, sparsely puberulous. **Leaves** alternate, evergreen; stipules narrowly triangular to deltoid, 0.4–1.1 mm long, persistent; petioles generally of uniform thickness and colour, 0.4–3 cm long, glabrate except sparsely puberulous when young, often with exfoliating cuticle; blades simple, narrowly elliptic to elliptic or oblanceolate, sometimes oblong-elliptic, 4.2–19.9 × 1.9–7.4 cm, subcoriaceous, both surfaces glabrate except sparsely puberulous on abaxial major veins when very young, base cuneate or obtuse, sometimes attenuate, margins remotely serrulate, apex usually cuspidate, sometimes acuminate, tip 0.4–1.4 cm long; venation pinnate, primary vein 1, secondary veins (4) 5–6(7) on each side of the midrib, brochidodromous, tertiary veins percurrent and somewhat reticulate near the midrib; stipels and glandular knobs absent adaxially at petiole apex; adaxial basilaminar extrafloral nectaries 2, narrowly oblong-elliptic to elliptic, oblong-obovate to broadly obovate, or round-deltoid (rarely circular or irregularly obovate), 1.3–3 × 0.4–1.8 mm; abaxial laminar extrafloral nectaries (2)–4(–14) per side, 0.2–0.6 mm in diam, near the margins on distal 2/3rds of the blade, adaxial laminar nectaries absent. **Inflorescences** axillary, bisexual racemose thyrses (often appearing unisexual due to protogynous development), 0.5–3.5 cm long, 1–2/axil; peduncle absent; axes glabrate to sparsely puberulous; staminate bracts ovate to broadly ovate, 0.5–0.9 mm long, glabrate to puberulous (sometimes only on the central vein and margin); pistillate bracts ovate, 0.6–0.9 mm long, glabrate to puberulous (sometimes only along the margin); staminate flowers numerous, distal, 1–2(3)/node in reduced and condensed cymules (rarely proximal cymules bisexual with a terminal pistillate flower); pistillate flowers 1, basal (may appear to arise from the leaf axil), or rarely 2–3, 1/node in proximal bisexual cymules, usually fallen or in fruit when staminate flowers are at or near anthesis. **Staminate flowers:** pedicel (2.5)9–13 mm long at anthesis, sparsely to densely puberulous; bud subglobose to ovoid, apex rounded; sepals 3, often recurved at anthesis, ovate, 1.2–1.5 × 0.8–1 mm, apex obtuse, abaxial surface sparsely to moderately puberulous (sometimes only near the apex); receptacle globose, fully covered with anthers; nectary an extrastaminal annular ring, sometimes appearing lobed or 3-segmented, or not evident; androecium subglobose, 0.5–0.6 × 0.6–0.8 mm, stamens 16–20, filaments absent (rarely present, stout, < 0.5 mm long, on ~3 basal-most stamens), anther sacs ellipsoid, dehiscing longitudinally. **Pistillate flowers:** pedicel (comprising cyme axis and true pedicel) 3–12.5 mm long, glabrate to sparsely puberulous; sepals 4, triangular to broadly triangular, sometimes lanceolate, 0.5–0.7 × 0.3–0.6 mm, glabrate to sparsely puberulous; ovary 4-lobed, 0.8–2 × 1.3–3.4 mm, lobes

rounded and laterally compressed, glabrate except often puberulous along midline of the lobe, conspicuous wings or horns absent; styles 4, entirely connate into a depressed-subglobose column, wider than long, sometimes donut-shaped, with a central dimple when young, 0.3–1 × 0.6–1.8 mm, unlobed distally, glabrate; stigmas 4, pale yellow or golden-brown when dry, round-deltoid (appearing clover-shaped as a group), 0.3–0.5 mm long each, smooth. **Fruits** 4-lobed capsules, 0.5–0.8 × 0.9–1.3 cm, surface verrucose, glabrate to very sparsely puberulous, each carpel subglobose, usually unornamented, sometimes with a short tubercle, 0.9–1.1 mm long; stylar columns persistent, depressed-subglobose with conspicuous clover-shaped stigmas, glabrate; pedicels 8.5–15 mm long. **Seeds** not seen. Figure 5.

Pollen—Tricolpate, oblate spheroidal (P/E = 0.88–1.0), polar axis 29.1–32.7 µm, equatorial axis 29.1–37.1 µm; amb subcircular; colpi broad, margins uneven and jagged; tectum coarsely reticulate (voucher: Lowrie et al. 6161 MO).

Etymology—The specific epithet is derived from *brevi-* (Latin, short or small) and *-styla* (Latin, -styled), and refers to the short stylar column that differentiates it from other neotropical species.

Distribution, Habitat, and Phenology—This species is known from the Rio Jarí region of northern Pará and a single collection from east-central Amazonas, Brazil (Fig. 6), suggestive of a more widespread distribution in the central and eastern Amazon basin. They are slender lianas climbing 3–6 m in terra firme rainforest, with elevations not recorded (estimated < 100 m), and flowering and fruiting specimens collected from July to October.

Discussion—*Plukenetia brevistyla* is morphologically similar to *P. megastyla* but differs by having short depressed-subglobose stylar columns, 0.3–1 mm long (Fig. 5), petioles with more or less uniform thickness (sometimes darker in colour at the base and apex), and subcoriaceous leaf blades, compared to thick oblong-obovoid stylar columns, 2.6–4.4 mm long, petioles with thickened, often purplish, pulvinus-like regions at the base and apex, and thick-chartaceous leaf blades in *P. megastyla*. Both species are distributed in the Amazon basin with *P. brevistyla* near the main stem of the Amazon River and *P. megastyla* along the southern boundary of the region (Fig. 6). The ETS phylogeny resolved *P. brevistyla* as an early diverging lineage in sect. *Penninervioae*, distinct from *P. megastyla* (Fig. 4). Both *P. brevistyla* and *P. megastyla* are vegetatively similar to *P. brachybotrya*, but the latter differs in its short massive globose stylar columns, 2–2.5 mm long (Fig. 3C), staminate flowers 1/node (compared to 1–3(4)/node), and primarily western Amazon distribution.

Staminate flowers of *P. brevistyla* show variation that falls within the typical range of sect. *Penninervioae*. All have sessile anthers densely packed on a globose or subglobose receptacle; however, variation was noted in the presence of a nectary and outer whorl of stamens with short filaments. An annular nectary was either consistently (Lowrie et al. 30) or variably present (Silva 2392). A third collection (Oliveira 4513) had a distinctly 3-lobed annular nectary and an outer whorl of ~3 stamens with very short filaments. Additional collections are needed to understand this variation in staminate flower morphology.

The NY sheet of Lowrie et al. 30 is unusual for having inflorescences with 2–3 pistillate flowers arising from the basal-most node, as well as for having proximal bisexual cymules that terminate with a pistillate flower. Remaining sheets of the

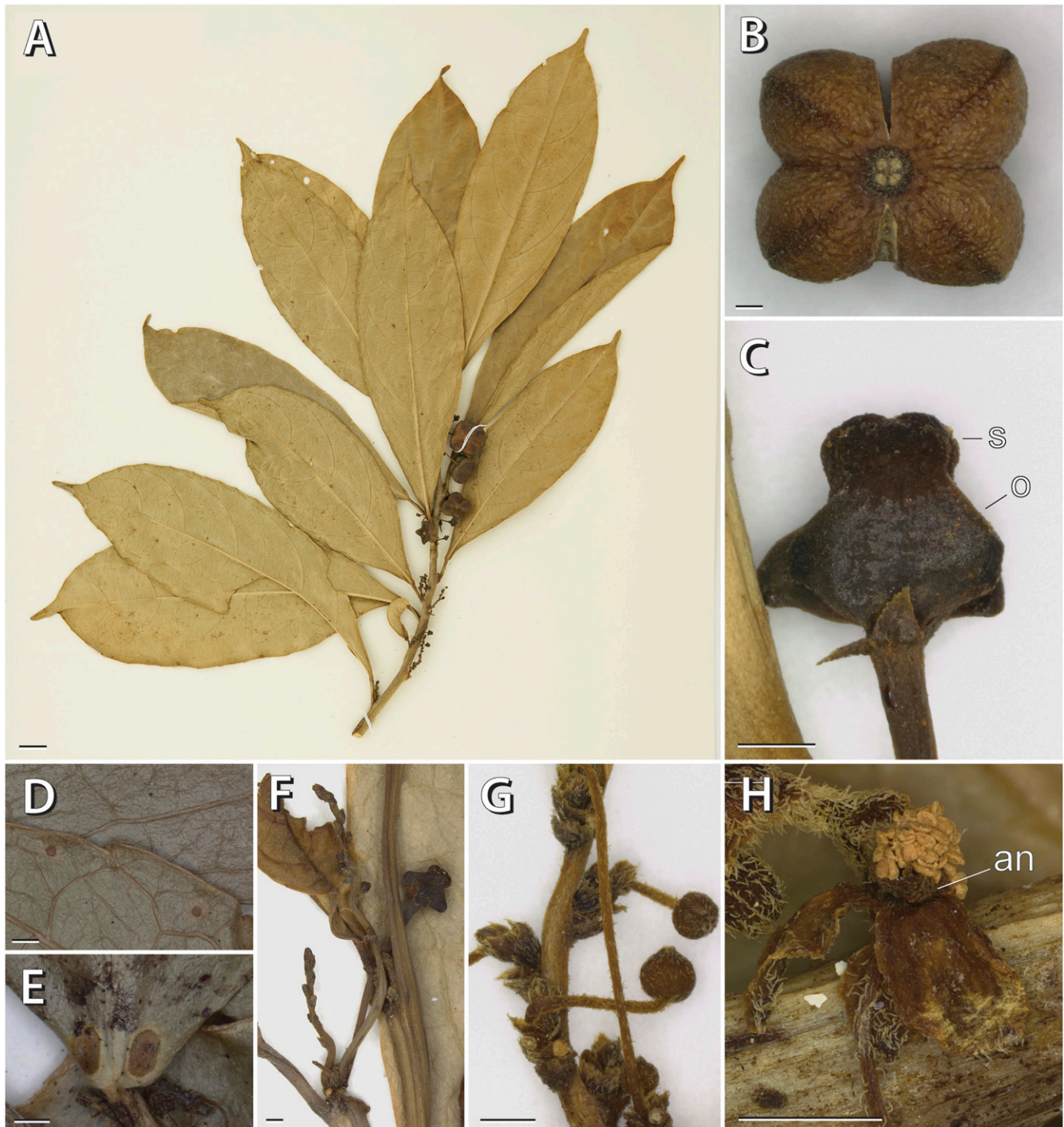


FIG. 5. *Plukenetia brevistyla* sp. nov. A. Branch with mature leaves, inflorescences, and fruit. B. Capsule. C. Pistillate flower. D. Abaxial leaf blade margin with laminar extrafloral nectaries. E. Adaxial leaf blade with basilaminar extrafloral nectaries. F. Close-up of inflorescences. G. Close-up of staminate cymules. H. Staminate flower. Photos by W. Cardinal-McTeague. Source: A, C, F–G. *Lowrie et al.* 30 (MO, NY); B. *Silva et al.* 1150 (NY); D–E, H. *Oliveira* 4513 (NY). (Abbreviations: an = annular nectary; o = ovary; s = style. Scale bars: A = 1 cm; B–H = 1 mm).

same collection (CAN, MO, US) have a single pistillate flower per inflorescence, which is typical for the species.

The collection *Oliveira* 3603 (NY01461552) co-occurs with *P. brevistyla* near Monte Dourado, Pará, but differs by having oblong-elliptic leaf blades and petioles with slightly thickened pulvinus-like regions at the base and apex, which is more typical of *P. megastyla*. There is insufficient floral material to confidently determine its identification, but we tentatively place this collection with *P. brevistyla* based on its location.

Specimens Examined—Brazil.—PARÁ: Rio Jari, Monte Dourado, ao lado do Campo de Aviação, 14 June 1968, *Oliveira* 4513 (NY); Rio Jari, Monte Dourado, 4 October 1968, *Silva* 1105 (CAN, NY, US); Jari, Estrada do Munguba, km 10, 10 July 1969, *Silva* 2392 (NY).

11. *Plukenetia chochoensis* L.J.Gillespie & Card.-McTeag. sp. nov. TYPE: COLOMBIA. Valle del Cauca: Buenaventura, Bajo Colima, road to Junchaco Palmeras, [3.91666°, -77.20000°], 100 m, 10 July 1984, A.H. Gentry, M. Monsalve B. & D.A. Wolfe 47799 (holotype: MO! [accession 3265264, barcode

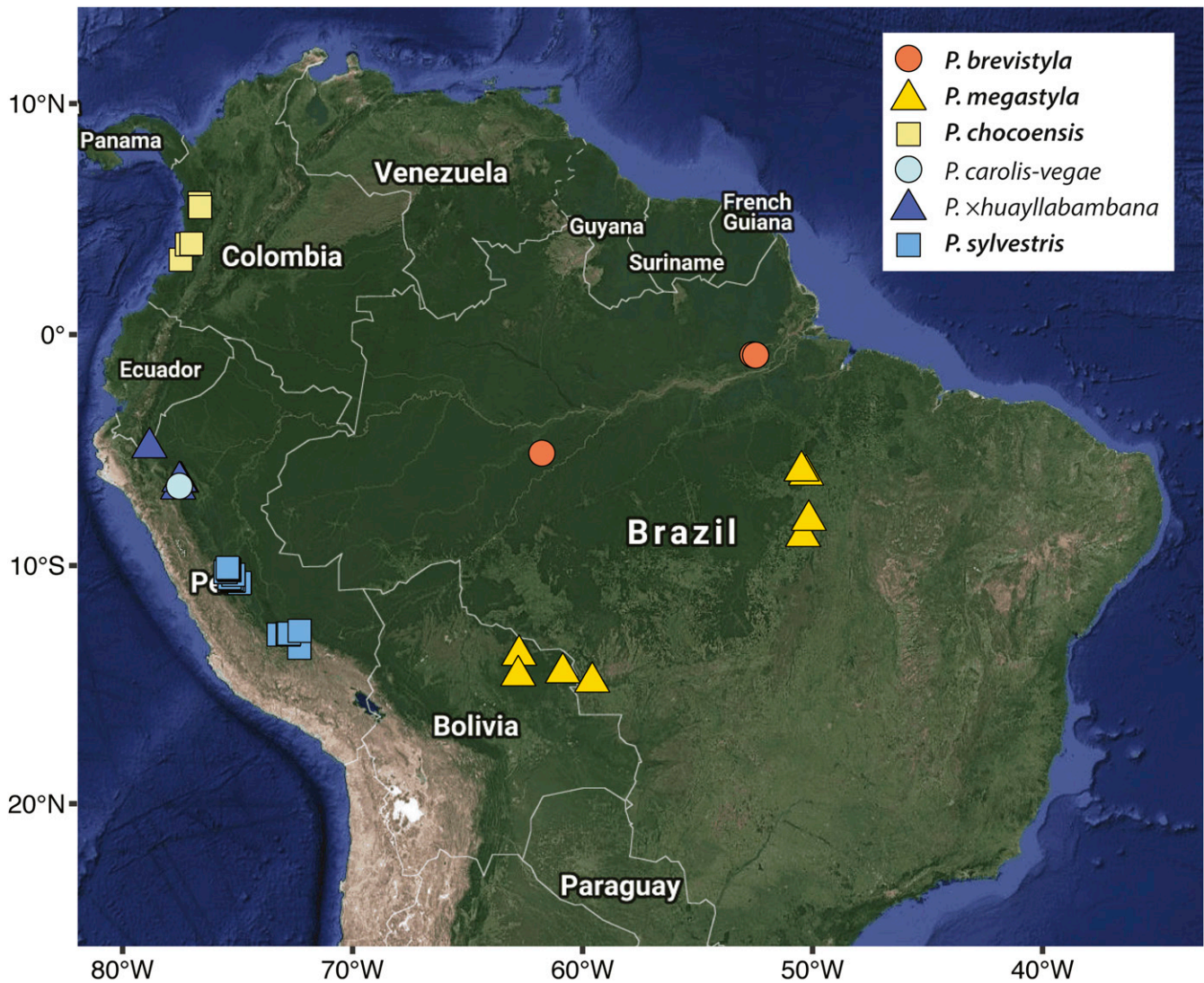


FIG. 6. Distribution map of our new species in sect. *Penninervia*, *P. brevistyla*, *P. chocoensis*, and *P. megastyla*, and members of the high elevation species complex in sect. *Plukenetia*, *P. carolis-vegae*, *P. xhuayllabambana*, and *P. sylvestris*. (Map data ©2019 Google, Imagery ©2019 NASA, TerraMetrics).

MO-1381711]; isotypes: COL [accession 540920, barcode COL000397503; image!], F [accession 1938863, barcode V0216686F; image!].

Similar to *P. penninervia* Müll.Arg. but differs in its elongate narrowly oblong-elliptic adaxial basilaminar extrafloral nectaries, presence of abaxial laminar extrafloral nectaries, and longer inflorescences.

Monoecious vines to slender lianas; stems erect or twining; old stems to 1.2 + cm in diam, bark dark purplish brown, coarsely striate; older flowering stems medium brown when dry, to ~5 mm in diam, faintly striate, puberulous to glabrate; younger stems faintly striate to striate, puberulous or pubescent. **Leaves** alternate, evergreen; stipules deltoid, 0.5–0.7 mm long, deciduous; petioles generally of uniform thickness and colour, 0.7–1.6 cm long, puberulous; blades simple, elliptic, oblong-elliptic, ovate-elliptic or obovate-elliptic (sometimes narrowly so), 8–16 × 3–6.5 cm, thick-chartaceous, drying shiny olive-green above, dull olive-green or pale olive-green with orange-brown veins below, both surfaces glabrous or glabrate with major veins glabrate to sparsely puberulous, base acute to obtuse, usually shortly attenuate around basilaminar extrafloral nectaries, margins serrulate with small glandular teeth, apex

acuminate to cuspidate, tip 0.6–1.3 cm long; venation pinnate, primary vein 1, secondary veins 5–7 on each side of the midrib, brochidodromous, tertiary veins percurrent (rarely reticulate); stipels and glandular knobs absent at petiole apex; adaxial basilaminar extrafloral nectaries 2, narrowly oblong or narrowly oblong-elliptic, sometimes irregular in shape, 2–4 × 0.5–1(–1.6) mm; abaxial laminar extrafloral nectaries 1–8/side, 0.3–0.7 (–0.9) mm in diam, 0.4–2 mm from margin on distal 5/6–1/10 of blade, adaxial laminar nectaries absent. **Inflorescences** axillary, bisexual racemose thyrses, 0.5–2 cm long at the pistillate flower stage, elongating up to 6 cm in the later staminate stage, 1(2)/axil; peduncle 0.1–0.2 mm long, elongating to 10 mm in later staminate and fruit stage; axes moderately or sometimes densely puberulous throughout; staminate bracts ovate-deltoid, 0.5–0.9 mm long, puberulous; pistillate bracts deltoid or ovate-deltoid, 0.7–1 mm long, puberulous; staminate and pistillate bracteoles similar but usually smaller; staminate flowers numerous, distal, ~3–12/node in condensed to racemose cymes (to 10 mm long); pistillate flowers 1, basal, fallen or in fruit when staminate flowers are at anthesis. **Staminate flowers**: pedicel 3–4.2 mm long at anthesis, moderately puberulous; bud subglobose, apex rounded to obtuse, often mucronate; sepals 3,

reflexed, elliptic or ovate-elliptic, $1\text{--}1.2 \times 0.6\text{--}0.8$ mm, apex obtuse, abaxial surface moderately puberulous; receptacle subglobose to globose, fully covered with anthers, on stalk to 0.3 mm long; nectary an interstaminal 3–6-segmented ring (often inconspicuous in bud); androecium subglobose, $0.4\text{--}0.5 \times 0.5\text{--}0.6$ mm, stamens 10–15, dimorphic, 3(4) basalmost with short filaments (0.2–0.3 mm long), alternating with sepals, emerging below and between the nectary segments and arching upwards, remaining 7–12 with filaments absent and densely packed on receptacle, anther sacs ellipsoid, dehiscing longitudinally. **Pistillate flowers:** pedicel 3–9 mm long (comprising cyme axis 1.5–6 mm + true pedicel 1.5–3.5 mm), moderately to densely puberulous, bracteoles 1/3 to 2/3 way along pedicel between cyme axis and true pedicel; sepals 4, triangular, $0.8\text{--}1.2 \times 0.5\text{--}0.8$ mm, sparsely puberulous to glabrate, margins hairy; ovary 4-lobed, $0.8\text{--}1.1 \times 1.4\text{--}2$ mm, puberulous or sparsely puberulous, lobes rounded and somewhat laterally compressed, 0.3–0.5 mm long, 0.8–1 mm wide at base, conspicuous wings or horns absent; styles 4, entirely connate into a thick cylindrical or obovoid-cylindrical column, $0.9\text{--}1.2 \times 0.8\text{--}1$ mm, base constricted or not, apex truncate-rounded, unlobed distally, glabrate; stigmas 4, round-deltoid to circular, each 0.5 mm long, smooth. **Fruits** 4-lobed capsules, ~ 1.5 cm wide, surface orange-brown, irregularly rugose-verrucose, glabrate, each carpel lobe subglobose, with a horizontally elongate or crescent-shaped tubercle, 2–3 mm wide, 0.5–0.6 mm high; pedicel ~ 18 mm long, including cyme axis 4–7 mm long, densely puberulous, true pedicel ~ 11 mm long, sparsely puberulous. **Seeds** (not well preserved, squashed) very broadly lenticular or subglobose?, ~ 7 mm in diam, with radial ridge, surface orange-brown to red-brown, with irregular cream blotches. Figure 7.

Etymology—The specific epithet is derived from the Chocó, the Biogeographic Region where it occurs, and the Colombian department where many collections are from.

Distribution, Habitat, and Phenology—This species is known from the central Chocó and eastern Valle del Cauca departments of Colombia, west of the Andes (Fig. 6). They are vines or slender lianas of tropical pluvial forest, growing in primary or disturbed primary forest, on shrubby vegetation, or along creeks from 10–100 m elevation. Flowering specimens were collected in January, February, May, and July; the single collection seen with fruit was collected in February. Field notes describe their flowers as green or brownish.

Discussion—Collections belonging to *P. chocoensis* were previously included within *P. penninervia*, but were noted as possibly representing a new species in the *P. penninervia* complex (Gillespie 1993). This species complex is characterized by staminate flowers with dimorphic stamens (outer with filaments, inner with anthers sessile on a subglobose receptacle) and often with a segmented annular nectary, pistillate flowers with a stout-cylindrical styler column and \pm elliptic leaf blades. Similar to *P. penninervia* in its leaf blade shape and presence of a single pair of basilar extrafloral nectaries, *P. chocoensis* differs in its larger, elongate, narrowly oblong or oblong-elliptic basilar nectaries (versus smaller and circular in *P. penninervia*), the blade attenuate basally around the basilar nectaries (versus not attenuate), presence of abaxial laminar extrafloral nectaries (versus usually absent), and margins with glandular teeth (versus with distinct rimmed circular glands or with both circular glands and glandular teeth). Blade colour (in the dried state) also differs, with *P. chocoensis* blades drying olive-green, with darker orange-

brown venation below, and *P. penninervia* blades typically drying grey-green, with paler cream or straw-coloured venation below. Petioles, stems, and inflorescence axes are moderately to densely short puberulous (versus sparsely to moderately puberulous to pubescent in *P. penninervia*) and staminate stage inflorescences are longer (1.5–6 cm versus 1–2 cm). The remaining species in the *P. penninervia* complex (*P. multiglandulosa* and *P. supraglandulosa*) are also distinguishable from *P. chocoensis*. *Plukenetia chocoensis* differs from *P. multiglandulosa* in having a single pair of basilar glands, puberulous petioles, and abaxial leaf blades glabrous or glabrate with major veins glabrate to sparsely puberulous (versus multiple pairs of basilar glands, densely hirsute petioles, and hirsute abaxial blades), and differs from *P. supraglandulosa* in the absence of laminar glands on the adaxial blade surface (versus present).

The segmented annular nectary of *P. chocoensis* appears to be usually 3-segmented, with each segment horizontally elongate and often 2-lobed. Sometimes one or more of these segments are fully divided into two, resulting in up to 6 segments per nectary.

In contrast to its morphological similarity to *P. penninervia*, molecular data suggests a relationship with three Amazonian and Guianan species. A previous molecular phylogeny based on two plastid (*matK*, *ndhF*) and five nuclear (ETS, ITS, *KEA1* introns 11 and 17, *TEB* exon 17) markers resolved *P. chocoensis* (referred to as *P. cf. penninervia*; Gentry et al. 47799) in a strongly supported clade with *P. brachybotrya*, *P. lorentensis*, and *P. verrucosa* (Cardinal-McTeague et al. 2019a; summarized in Fig. 1). This suggests that the *P. penninervia* complex is paraphyletic and that dimorphic stamens and stout-cylindrical styles may be plesiomorphic characters in sect. *Penninerviae*.

Several collections from Cerros del Cuchillo in the Urabá area of northern Chocó department (Cardenas 1675, 1748, 1903) are here referred to *P. penninervia*, but need further study. They differ from *P. chocoensis* in their elliptic basilar extrafloral nectaries, absence of abaxial laminar extrafloral nectaries, presence of distinct circular nectaries on the blade margin, longer pubescence on stems and petioles, longer narrowly triangular staminate bracts, and longer pistillate sepals.

Specimens Examined—**Colombia**.—CHOCÓ: Municipio de Quibdó, bosque frente al barrio Obrero, [5.708333°, -76.65389°], 24 May 1985, Espina & Garcia 1533 (COL [accession 283420, barcode COL000395807; image], F [accession 1982641, barcode V0216685F; image], MO [accession 3292704, barcode MO-1381696]); Road to Loró (under construction) 1–2 km SE of Yuto, ca. 30 km S of Quibdó, [5.53833°, -76.63472°], 80 m, 7 January 1979, Gentry & Renteria 23761 (COL [accession 206142, barcode COL000395801; image], MO [accession 2717121, barcode MO-1381700]); Road (under construction) to Llorá from Yuto, pluvial forest, along creek ca. 2 km E of Yuto, [5.53333°, -76.63333°], 50 m, 18 January 1979, Gentry & Renteria 24367 (COL [accession 223108, barcode COL000395803; image], MO [accession 2716706, barcode MO-1381701]).—VALLE DEL CAUCA: Costa del Pacífico, río Naya, Puerto Merizalde, 5–20 m, 20–23 February 1943, Cuatrecasas 14006 (F [accession 1358438, barcode V0216684F; image], F [accession 1358485, barcode V0216683F; image], US [accession 2815114, barcode 01298527], US [accession 2815115, barcode 01298528]); Costa del Pacífico, río Cajambre, 5–80 m, 5–15 May 1944, Cuatrecasas 17472 (F [accession 1358549, barcode V0216687F; image], F [accession 1358550, barcode V0194071F; image], US [accession 2817383, barcode 01298562]); Puerto Merizalde, Río Nanay, forest behind town, [3.25000°, -77.46666°], 10 m, 22 Feb 1983, Gentry & Juncosa 40563 (COL [accession 263437, barcode COL000395806; image], F [accession 1988829, barcode V0216682F; image], MO [accession 3031302, barcode MO-1381713]); Buenaventura, Bajo Calima, Pulpapel logging concession SE of Buenaventura, [3.95000°, -77.00000°], 100 m, 22 January 1986, Stein et al. 3260 (MO [accession 3490284, barcode MO-1381712]).

12. PLUKENETIA LORENTENSIS Ule, Verh. Bot. Vereins Prov. Brandenburg 50: 81. 1908. *Apodandra lorentensis* (Ule) Pax &

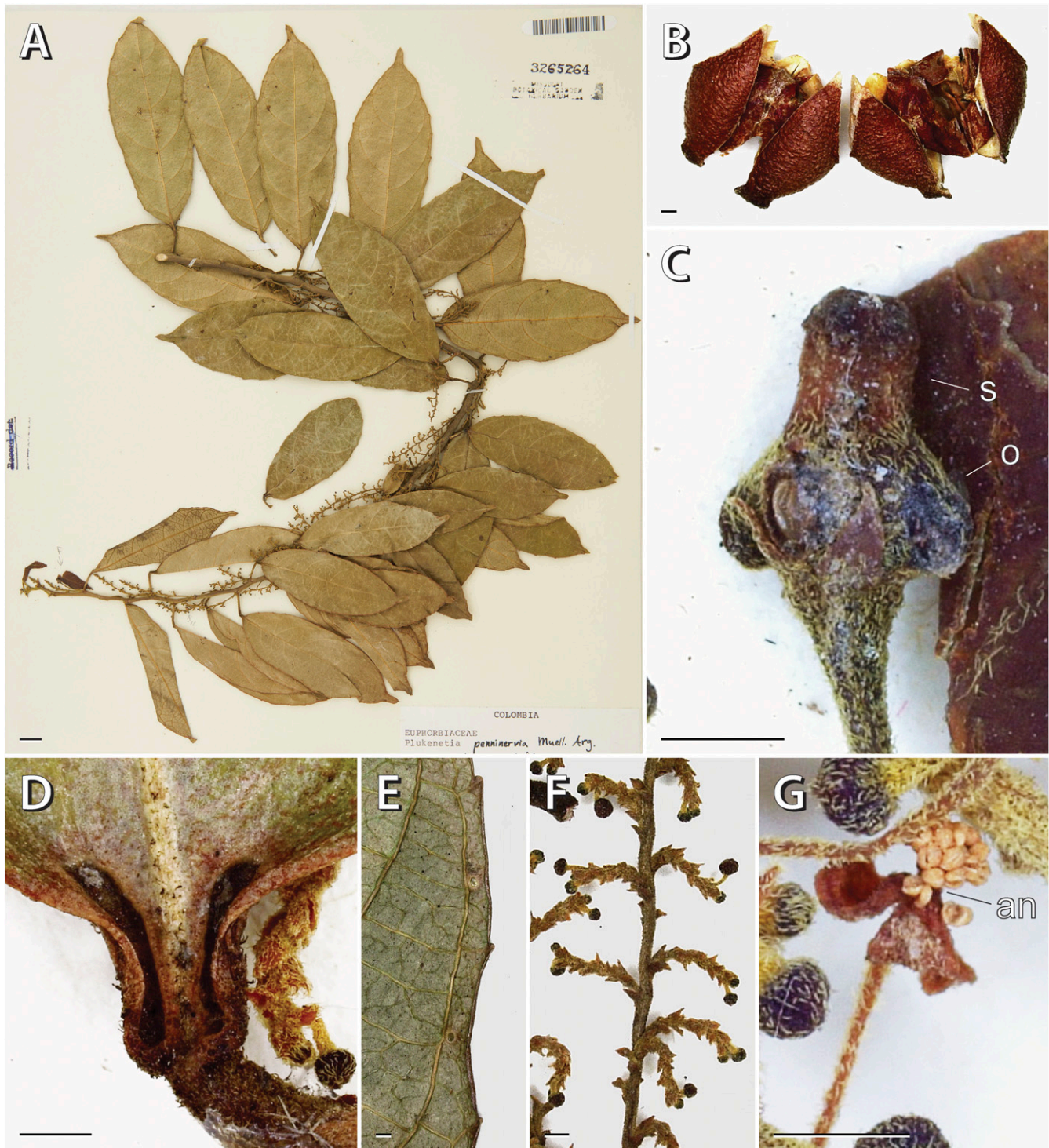


FIG. 7. *Plukenetia chocoensis* sp. nov. A. Branch with mature leaves and inflorescences. B. Capsule fragments. C. Pistillate flower. D. Adaxial leaf blade with basilar extrafloral nectaries. E. Abaxial leaf blade margin with laminar extrafloral nectaries. F. Close-up of staminate cymules. G. Staminate flower. Photos by W. Cardinal-McTeague. Source: A, C–G. *Gentry et al.* 47799 (MO); B. *Cuatrecasas* 14006 (US). (Abbreviations: an = annular nectary; o = ovary; s = style. Scale bars: A = 1 cm; B–G = 1 mm).

K.Hoffm. in A.Engler (ed.), *Pflanzenr.* IV, 147, IX (Heft 68): 21. 1919. TYPE: PERU. Iquitos, April 1903, *E. Ule* 6837 (holotype: B [destroyed]; lectotype designated here: L [accession 601470, barcode L 0137704; image!]; isolectotypes: F! [accession 767223, barcode V0042476F; fragment ex G], G! [barcode G00441994], HBG [barcode HBG-515850; image!], MG [barcode MG006665; image!]).

Apodandra corniculata Cardiel, *Revista Acad. Colomb. Ci. Exact.* 18(71): 469. 1993. Type: Colombia. Caquetá, Sierra de Chiribiquete. Campamento Norte. Recorrido por el cauce casi seco de un arroyo al NE del campamento, [1.11667°, -72.83333°], 350–500 m, 13 December 1990 [misabeled as 1991 on sheets], *S. Castroviejo, J.M. Cardiel, G. Galeano & F. González* 12042 (holotype: COL [accession 365413, barcode COL000002059;

image!]; isotypes: COAH, COL [accession 365412, barcode COL000002060; image!], G [barcode G00434095; image!], MA [barcodes MA 509696, MA 509696-2; images!], US [accession 3303795, barcode 00433407; image!].

Notes—See Gillespie (1993) for species discussion and Gillespie and Armbruster (1997) for species description. We report one new addition to the distributions given in Gillespie (1993) and Gillespie and Armbruster (1997): Pará, Brazil (*Ramos 1105*).

The holotype was destroyed at B so a new lectotype is designated from the isotype housed at L. This specimen has the most abundant and intact floral and vegetative material among the available isotypes.

Here, we treat *Apodandra corniculata* as a synonym of *P. lorentensis*. Cardiel Sanz (1993) distinguished this species from *P. lorentensis* on the basis of having leaf blades with 5–7 secondary veins and staminate flowers with 20–25 stamens; however, these characters are within the range of variation observed in *P. lorentensis* (Gillespie and Armbruster 1997; new observations). Additionally, the collection date on the type labels of *A. corniculata* are mislabeled as 1991, but the expedition is reported elsewhere on the label and in the manuscript as occurring in 1990 (Cardiel Sanz 1993).

13. *Plukenetia megastyla* Card.-McTeag. & L.J.Gillespie sp. nov. TYPE: BOLIVIA. Depto. Santa Cruz, Prov. Guarayos (formerly Prov. Nuflo de Chavez), 4 km N of Perseverencia, [-14.68333°, -62.80000°], 275 m, 9 September 1990, M.H. Nee 38682 (holotype: NY! [barcode 02286564]; isotype: MO! [accession 3816603, barcode MO-2001411]).

Similar to *P. brachybotrya* Müll.Arg. and *P. brevistyla* Card.-McTeag. & L.J.Gillespie, but differs by having an oblong-obovoid styler column with a truncate apex, 2.6–4.4 mm long.

Monoecious vines to slender lianas; stems erect or twining; older stems light brown and tan when dry, to ~5 mm in diam, striate, glabrate; younger stems smooth to striate, puberulous. **Leaves** alternate, evergreen; stipules narrowly triangular to deltoid, 0.3–1 mm long, persistent; petioles with thickened, often purplish, pulvinus-like regions at the base and apex, entire petiole 0.7–3.5 cm long, glabrate except sparsely puberulous when young; blades simple, narrowly elliptic to elliptic, oblong-elliptic, oblanceolate-elliptic, or obovate-elliptic (rarely ovate-elliptic), 7–19.8 × 1.8–7.5 cm, thick-chartaceous, both surfaces glabrate except sparsely puberulous on abaxial major veins when very young, base cuneate to obtuse, margins remotely serrulate, apex usually cuspidate, sometimes acuminate or attenuate, tip 0.4–1.6 cm long; venation pinnate, primary vein 1, secondary veins 5–7(–9) on each side of the midrib, weakly brochidodromous, tertiary veins percurrent, sometimes reticulate towards the midrib; stipels and glandular knobs absent adaxially at petiole apex; adaxial basilaminar extrafloral nectaries 2, narrowly to broadly oblong-elliptic, obovate, round-deltoid, or sometimes irregularly obtriangular, rarely with an additional smaller nectary above, 1.0–2.4 × 0.4–1.7 mm; abaxial laminar extrafloral nectaries (3–)6–14 per side (rarely absent), 0.2–0.7 mm in diam, near the margins on distal 9/10th to 4/5th of the blade, adaxial laminar nectaries absent. **Inflorescences** axillary, bisexual racemose thyrses, 0.6–3 cm long, 1(2)/axil; peduncle absent (rarely 0.2–0.3 mm long); axes very sparsely to moderately puberulous throughout (sometimes more puberulous distally); staminate bracts ovate to broadly ovate, 0.4–1.1 mm long, puberulous (sometimes only along the margins and at the apex); pistillate bracts ovate, sometimes deltoid, (0.3–) 0.7–1 mm long, sparsely to densely puberulous; staminate

flowers numerous, distal, 1–3(4)/node in condensed cymes (appearing short racemose if 3–4 flowers); pistillate flowers 1, basal (may appear to arise from the leaf axil), usually fallen or in fruit when staminate flowers are at or near anthesis. **Staminate flowers:** pedicel 12.8–14.8 mm long at anthesis, sparsely puberulous (densely when young); bud subglobose to ovoid, sometimes depressed and wider than long, apex rounded; sepals 3–4, incurved to spreading at anthesis, ovate to broadly ovate, 1–2.4 × 0.5–1.7 mm, apex obtuse, abaxial surface sparsely to moderately puberulous; receptacle subglobose to globose, fully covered with anthers; nectary an extrastaminal annular ring, upper surface sometimes undulate or uneven; androecium subglobose, 0.6–0.9 × 0.8–1.3 mm, stamens 20–30, filaments absent, anther sacs ellipsoid, dehiscing longitudinally. **Pistillate flowers:** pedicel (comprising cyme axis and true pedicel) 12.9–24.7 mm long, glabrate to sparsely puberulous; sepals 4, triangular, sometimes deltoid to broadly triangular, 0.5–1.2 × 0.4–0.7 mm, puberulous; ovary 4-lobed, 0.8–1.7 × 1–2 mm, lobes rounded and laterally compressed, glabrate except puberulous along midline of the lobe, conspicuous wings or horns absent; styles 4, entirely connate into an oblong-obovoid column, 2.6–4.4 × 2.6–3.7 mm, base constricted and 0.9–1.6 mm wide, apex truncate, with a central dimple when young, unlobed distally, glabrate; stigmas 4, light yellow-brown/tan or purple-red when dry, round-deltoid to circular, 0.8–1.1(2) mm long each, smooth. **Fruits** 4-lobed capsules, 0.7–1.1 × 1–1.6 cm, surface irregularly verrucose, glabrous or glabrate, each carpel lobe subglobose, usually with a short tubercle 0.4–1.4 mm long, sometimes unornamented; styler columns persistent, oblong-obovoid, apex truncate and dilated; pedicel (comprising cyme axis and true pedicel) (12)25–35 mm long. **Seeds** broadly lenticular, laterally compressed, elliptic to circular in outline, 4.8–5.2 × 5–5.9 × 3.8–4.2 mm, surface light to golden brown, sometimes with dark brown irregular splotches, weakly rugulose; testa persistent. Figure 8.

Pollen—Tricolpate, oblate spheroidal ($P/E = 0.88–1.1$), polar axis 32.9–45 μm , equatorial axis 31–51 μm ; amb sub-circular; colpi broad, margins uneven and jagged; tectum coarsely reticulate (voucher: *Sperling et al. 6161* CAN).

Etymology—The specific epithet is derived from *mega-* (Greek, large or great) and *-styla* (Latin, -styled), and refers to the large styler columns that differentiate this from similar species.

Distribution, Habitat, and Phenology—This species is known from two disjunct ranges in the southern Amazon basin: 1) Brazil, in southeastern Pará; and 2) Bolivia, in eastern Beni and Santa Cruz, and Brazil, in western Mato Grosso (Fig. 6). They are slender lianas climbing on trees in terra firme rainforest with high canopies, growing in primary or disturbed primary forest along trails or forest edges, on flat lands or low hills from 140–738 m elevation. Flowering and fruiting specimens were collected from February to November in Pará and from August to November in Mato Grosso and Bolivia.

Discussion—*Plukenetia megastyla* is morphologically similar to *P. brevistyla* but differs by having thick oblong-obovoid styler columns, 2.6–4.4 mm long (Fig. 8), petioles with thickened, often purplish, pulvinus-like regions at the base and apex, and thick-chartaceous leaf blades, compared to short depressed-subglobose styler columns, 0.3–1 mm long (Fig. 5), petioles with more or less uniform thickness (sometimes darker in colour at the base and apex), and subcoriaceous leaf blades in *P. brevistyla*. Additionally, the annular nectary of *P. megastyla* appears to be consistently present (Fig. 8G), whereas the nectary of *P. brevistyla* is variable and can be annular, 3-lobed, or not evident. Both species are distributed in

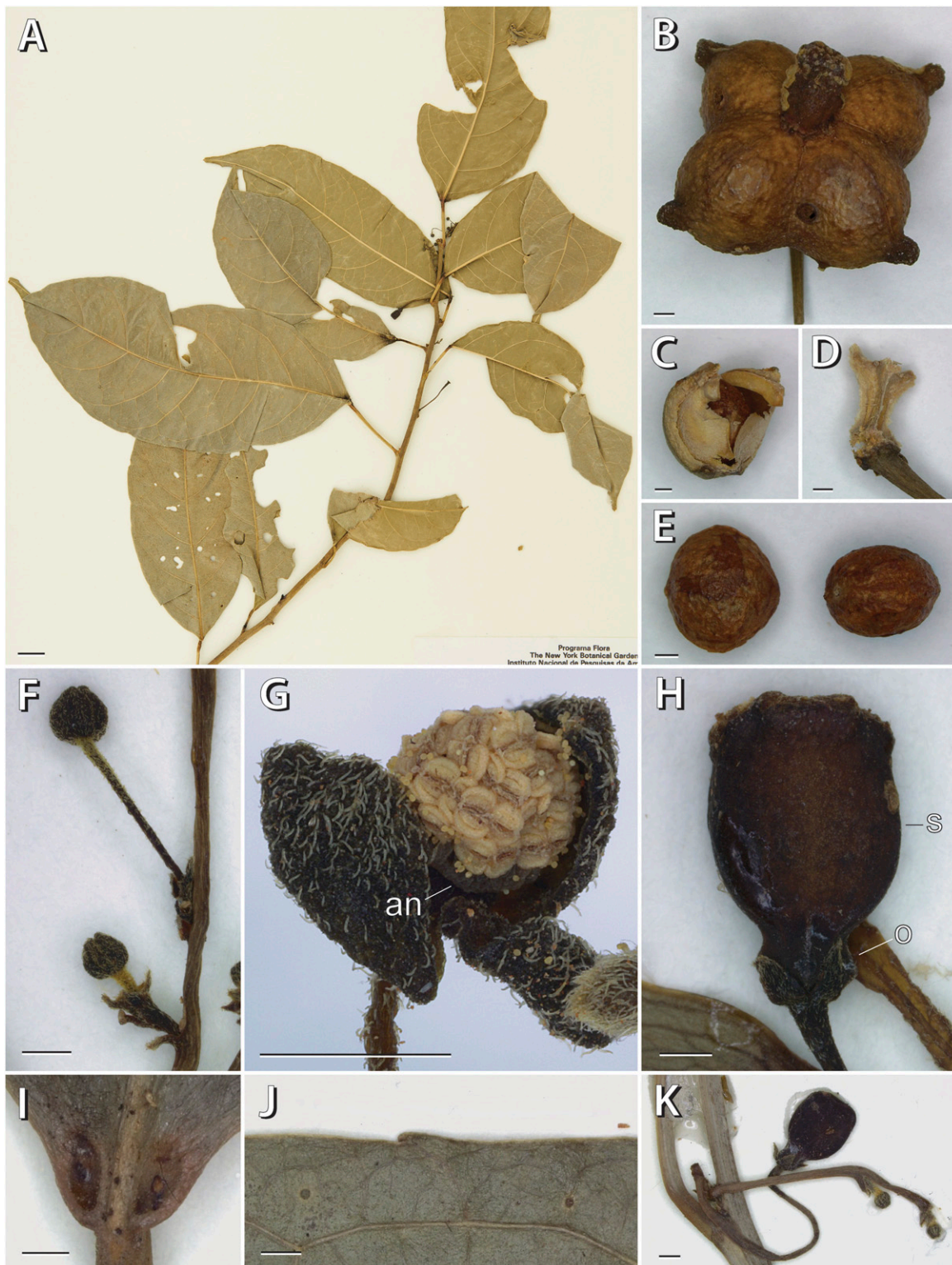


FIG. 8. *Plukenetia megastyla* sp. nov. A. Branch with mature leaves and inflorescences. B. Capsule. C. Capsule segment with seed. D. Columella. E. Seed, lateral view (left), ventral view (right). F. Close-up of staminate cymules. G. Staminate flower. H. Pistillate flower. I. Adaxial leaf blade with basilar nectaries. J. Abaxial leaf blade margin with laminar nectaries. K. Close-up of inflorescence. Photos by W. Cardinal-McTeague. Source: A, G. *Silva et al.* 6161 (NY); B, I–J. *Plovman* 8741 (NY); C–E. *Ledezma et al.* 921 (CAN); F, H, K. *Nee* 38682 (NY). (Abbreviations: an = annular nectary; o = ovary; s = style. Scale bars: A = 1 cm; B–K = 1 mm).

the Amazon basin, with *P. megastyla* along the southern boundary of the region and *P. brevistyla* near the main stem of the Amazon River (Fig. 6). A previous molecular phylogeny based on two plastid (*matK*, *ndhF*) and five nuclear (ETS, ITS,

KEA1 introns 11 and 17, *TEB* exon 17) markers resolved *P. megastyla* (referred to as *P. aff. brachybotrya*; *Ledezma et al.* 921, *Sperling et al.* 5873, 6161) in a strongly supported clade with *P. supraglandulosa* (Cardinal-McTeague et al. 2019a;

summarized in Fig. 1). The ETS phylogeny of this study recovered *P. megastyla* in a poorly resolved polytomy within sect. *Penninerviae*, distinct from *P. brevistyla* (Fig. 4). Both *P. megastyla* and *P. brevistyla* are vegetatively similar to *P. brachybotrya*, but the latter differs in its short massive globose styler columns, 2–2.5 mm long (Fig. 3C), staminate flowers 1/node (compared to 1–3(4)/node), and primarily western Amazon distribution.

Sperling et al. 5873 (NY1461553) is unusual for having an aberrant pistillate flower with a slender-cylindrical styler column and dilated apex. A younger pistillate flower on the sheet appears to have the typical oblong-obovoid styler column.

Specimens Examined—**Bolivia**. —BENI: Prov. Iténez, Canton Mateguá, Campamento móvil Cerro Azul ubicado a 30 km de la Comunidad de Tiquin, [-13.816°, -62.761°], 738 m, 4 November 2006, *Ledezma et al.* 921 (CAN, MO [accession 6057037, barcode MO-2115208]). —SANTA CRUZ: Prov. Velasco, Los Fierros, la senda hacia la meseta adentro bosque alto, [-14.558°, -60.861°], 200 m, 20 August 1996, *Jardim et al.* 3336 (MO [accession 04850338, barcode MO-1706758]). **Brazil**. —MATO GROSSO: Mun. Vila Bela da Santíssima Trindade, 41 km NNW of Pontes e Lacerda on BR364 to Vilhena, [-14.950°, -59.583°], 31 October 1985, *Thomas et al.* 4732 (NY [barcode 010064912]). —PARÁ, Mun. Conceição do Araguaia, range of low hills ca. 20 km west of Redenção, near São João and Troncamento Santa Teresa, approx. [-8.050°, -50.167°], 350–620 m, 12 February 1980, *Plowman et al.* 8741 (NY [barcode 01461555]); Mun. Conceição do Araguaia, 100 km south of Redenção on road (PA-150) to Barreiras dos Campos, Fazenda Inajaporã between Rio Inajazinho and Rio Inajá, approx. [-8.750°, -50.417°], 210 m, 19 February 1980, *Plowman et al.* 8908 (NY01461551); Serra dos Carajás, 1–4 km along road from camp AZUL toward AMZA camp N-1, [-6.100°, -50.283°], 550–600 m, 28 May 1982, *Sperling et al.* 5873 (MO [accession 4249342, barcode MO-2001412], NY [barcode 1461553]); Serra dos Carajás, 2–10 km southeast of ferry crossing on Rio Itacaiúnas, [-5.917°, -50.483°], ca. 225 m, 14 June 1982, *Sperling et al.* 6161 (CAN, MO [accession 4247783, barcode MO-2001413], NY, US).

14. PLUKENETIA MULTIGLANDULOSA Jabl., Mem. New York Bot. Gard. 17 (1): 143. 1967. TYPE: VENEZUELA. Amazonas: Cerro Parú, base of escarpment southward from camp 2 km, 1800 m, 12 February 1951, *R.S. Cowan & J.J. Wurdack* 31400 (holotype: NY! [barcode 00273179]; isotypes: F [accession 1702715, barcode V0057060F; image!], NY! [barcode 00273180], US! [accession 2620759, barcode 00096451]).

Notes—See Gillespie (1993) for species discussion.

15. PLUKENETIA PENNINERVIA Müll.Arg., Linnaea 34: 158. 1865. TYPE: MEXICO. Nueva España, Herb. Pavon [mislabelled specimen of *M. Sessé & J.M. Mociño* 4212] (lectotype designated here: G [barcode G00418847; image!]; isolectotypes [labeled *M. Sessé & J.M. Mociño* 4212] MA [barcodes MA 602300, MA 602301, MA 602302, MA 602303, MA 602304; images!]). Remaining syntype: VENEZUELA. [Aragua (fide Todzia 1989)]: Near Biscaina, 3000 ft [~900 m], 1860, *A. Fendler* 2412 (G-DC! [barcode G00313655; photo at F!], GH! [barcode 00048692], GOET [barcode GOET003663; image!], K! [barcode 000600747], PH [accession 611118, barcode 00030713; image!]).

Plukenetia angustifolia Standl., Publ. Field Columb. Mus., Bot. Ser., 4 (8): 314. 1929. TYPE: HONDURAS. Lancetilla Valley, near Tela, Department of Atlántida, 20–600 m, 6 December 1927–20 March 1928, *P.C. Standley* 56708 (holotype: F! [accession 581511, barcode V0057059F]; isotypes: A!, K!, US! [accession 1409360, barcode 00096449]).

Notes—See Gillespie (1993) for species discussion.

Taxonomic Discussion—*Plukenetia penninervia* can be divided into two informal groups united by geography and subtle differences in fruit/seed size. The first is a Mexican group that is widely distributed from southern Mexico to Panama and has

average sized seeds and fruits. The second is a Venezuelan group distributed primarily in that country, which differs by having slightly larger seeds and fruits (similar to *P. chocoensis*; “medium” sized seeds sensu Cardinal-McTeague et al. 2019a). The Mexican group might also more frequently lack annular nectaries in its staminate flowers, but this character needs to be investigated in greater detail. To complicate matters, there is evidence of a putative ancient hybridization event that resulted in the introgression of an ancestral plastid genome of *P. chocoensis*/*P. lorentensis* into the southern population of the Mexican group, specifically within a specimen from central Panama (*G. McPherson* 8461) (Cardinal-McTeague et al. 2019a, Fig. S3). It is unclear if the Venezuelan group (not yet sampled in phylogenetic studies) shares this same hybridization event or whether it should be considered a distinct taxon.

The two syntypes of *P. penninervia* correspond with these geographical groupings, *A. Fendler* 2412 from Venezuela and a “Herb. Pavon” collection from Mexico. Although José Pavón, of Ruiz and Pavón, most famously collected in Peru (and not Mexico), he is noted for selling duplicates of Sessé and Mociño’s Mexican collections to other herbaria in Europe, where they frequently lost their association with Sessé and Mociño and were attributed as “Herb. Pavón, Nueva España” (McVaugh 2000). Indeed, there are five sheets of *P. penninervia* at MA (*M. Sessé & J.M. Mociño* 4212) that are physical matches with the “Herb. Pavón” sheet at G (G00418847), which we hereby consider the same collection. To maintain the taxonomic stability of *P. penninervia* we designate the Mexican syntype (representing the cohesive and widespread Mexican group) as the lectotype collection for the species, selecting the recently rediscovered “Herb. Pavon” G specimen (L. Gautier pers. comm.) as lectotype. Future studies will need to investigate the morphology and phylogeny of the Venezuelan group, test if it exhibits plastid genome introgression, and determine if it should be recognized as its own species or subspecies.

The *P. penninervia* complex, characterized by dimorphic stamens, short cylindrical styles, and ± elliptic leaf blades, is proving to be taxonomically challenging and more speciose than previously thought. The complex is widespread from Mexico to northern South America, and comprises at least four species, *P. chocoensis*, *P. multiglandulosa*, *P. penninervia*, and *P. supraglandulosa*. Apart from our newly described Colombian species (*P. chocoensis*), several additional collections from Colombia, Ecuador, and Peru appear to belong to the *P. penninervia* complex and are tentatively placed in *P. penninervia*. Collections from northern Chocó department (*Cardenas* 1675, 1748, 1903) are here referred to as *P. penninervia*, but require further study (see the discussion of *P. chocoensis* for how these collections differ). Three collections from Pastaza province, Ecuador (Gillespie 1993) and one specimen from Cajamarca province, east of the Andes in northern Peru (*Vásquez* 25223) have the dimorphic stamens of the *P. penninervia* complex, but are well south of its known range. A thorough study of the *P. penninervia* complex in northern South America is needed, together with additional collections, to determine if these disjunct populations represent new taxa.

16. PLUKENETIA SUPRAGLANDULOSA L.J.Gillespie, Syst. Bot. 18 (4): 598. 1993. TYPE: FRENCH GUIANA. Sommet Tabulaire, zone centrale, versant occidental, ca. 40 km SE de Saül, 650 m, 27 August 1980, *J.J. de Granville* 3626 (holotype: US! [accession 3274039, barcode 00433067]; isotypes: CAY!, U! [barcode U 0002068], US! [accession 3285607, barcode 00646987]).

Notes—See Gillespie (1993) and Gillespie and Armbruster (1997) for species descriptions. Described originally from French

Guiana and Amapá, Brazil (Gillespie 1993), a more recent collection (Clark & Hoffman 622 US) extends the range west to Guyana.

17. *PLUKENETIA VERRUCOSA* Sm., Nova Acta Regiae Soc. Sci. Upsal., ser. 2, 6: 4. 1799. TYPE: SURINAME. *Linn. Collection of Surinam plants, No. 146* (holotype: LINN-HS [accession 1489.2; image!]).

Plukenetia volubilis L.f., Suppl. Pl. 421. 1781 publ. April 1782, nom. illeg. TYPE: SURINAME. Herb. Alstroemerii 1848, C.G. Dahlberg s.n. (holotype: S [accession S09-18958; image!]).

Plukenetia integrifolia Vahl, *Eclóg. Amer.* 3: 43. 1807. TYPE: GUYANA. Demerari, J.P.B. von Rohr 86 (holotype: C [barcode C10011347; image!]).

Notes—See Gillespie (1993) for species discussion and Gillespie and Armbruster (1997) for species description. Molecular phylogenetic analyses confirmed the previous hypothesis (Gillespie 1993) that the 3-veined cordiform leaves of *P. verrucosa* are a derived condition within the pinnately veined clade (subclades P1 + P2) (Fig. 1; Cardinal-McTeague et al. 2019a).

Taxonomic Discussion—Linnaeus f. (1781 publ. 1782) was the first to suggest there was a second species of *Plukenetia* from the Neotropics when he described the morphology of a new collection of *P. volubilis* from Suriname. However, there was no indication that Linnaeus f. meant for this to be a new species and it appears that he was expanding the concept of *P. volubilis* with the morphological variation found in Suriname (Dalberg s.n. S). Regardless, if we treat *P. volubilis* L.f. as a new species, it would be a homonym of *P. volubilis* L. and therefore illegitimate. As such, Smith (1799) was the first to provide a legitimate name, *P. verrucosa* Sm., for the new species from Suriname. Smith (1799) recognized that the description of *P. volubilis* in Linnaeus f.'s *Supplementum Plantarum* (1781 publ. 1782) was associated with *P. verrucosa*, but by convention, type status would be conferred to the specimen listed in Smith's herbarium (*Linn. collection of Surinam plants No. 146* LINN-HS).

- VI. *PLUKENETIA* sect. *PLUKENETIA*. *Sajorium* sect. *Pluknetia* Baill., *Étude Euphorb.* 483. 1858. TYPE: *Plukenetia volubilis* L.

Plukenetia sect. *Cylindrophora* Müll.Arg., *Linnaea* 34: 157. 1865. TYPE: *Plukenetia peruviana* Müll.Arg. [= *Plukenetia volubilis* L.]

Lianas or canopy lianas, stems slender to thick. **Leaf venation** palmate, primary veins 3. **Inflorescences** bisexual racemose thyrses (rarely racemes; usually unisexual in *P. polyadenia*); pistillate flowers solitary at 1–4 basal-most nodes; staminate flowers (1–) 3–15(–18)/node in condensed cymules, glomerules, or moderately condensed cymules with conspicuous and irregularly branched cyme axes (rarely 1/node). **Staminate flowers:** receptacle conical or globose; nectaries of interstaminal slender-cylindrical, ligulate, or small or large irregularly shaped segments (absent in *P. volubilis*); stamens 12–40, densely packed; filaments short-conical or slender-cylindrical, 0.5–3 mm long; pollen P = 48–60 µm, E = 53–69 µm, tectum foveolate. **Pistillate flowers:** styles (20–40)70–95% connate into a cylindrical column, 5.6–13.4(–35) mm long. **Fruits** 4(–7)-lobed or subglobose-quadrangular capsules, dry, dehiscent or semi-dehiscent, (1.6–)2.5–10 cm in diam, or subglobose-quadrangular berries, fleshy, indehiscent, 3.5–11 cm in diam. **Seeds** broadly lenticular to lenticular (ovoid or triangular-ovoid in *P. polyadenia*), 10–34.3(49–56) × 8–27(33–37) × (2.5–9)14–36 mm (“medium,” “large,” “extra-large,” or “maximum,” sensu Cardinal-McTeague et al. 2019a).

The species in this section are distributed in Mexico, Central America, northwestern and Amazonian South America, and the Lesser Antilles.

Discussion—Section *Plukenetia* refers to subclade P3 (Fig. 1) and includes eight species distributed in the Neotropics. The section is morphologically similar to sect. *Angostylidium* but differs in its neotropical distribution and having cylindrical stylar columns with free style arms that are more or less uniform in thickness or tapered and erect or spreading (Fig. 3G–K). Section *Plukenetia* is also distinct in having staminate flowers with long slender-cylindrical filaments and interstaminal nectaries (although with short-conical filaments and without nectaries in *P. volubilis*), and exhibiting the widest range of fruit type (dry or fleshy, and dehiscent, semi-dehiscent, or indehiscent) and seed size (“medium” to “maximum” sized).

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

1. Styles (9–)15–35 mm long; filaments short-conical, ~0.5 mm long; interstaminal nectaries absent. 25. *P. volubilis*
1. Styles 4–12 mm long; filaments slender-cylindrical, 0.5–3 mm long; interstaminal nectaries present (small and sometimes overlooked in *P. stipellata*). 2
2. Fruits 1.6–3 cm in diam, dry; interstaminal nectaries of small irregularly shaped segments; stipels 2 and glandular knob absent adaxially at petiole apex. 23. *P. stipellata*
2. Fruits 2.5–11 cm in diam, dry or fleshy; interstaminal nectaries slender-cylindrical, ligulate (strap-shaped), or large irregularly shaped segments; stipels 0–2 and glandular knob 0 or 1 adaxially at petiole apex. 3
3. Interstaminal nectaries of large irregularly shaped segments; leaves: lateral primary veins arching towards the margins $\leq 1/2$ the length of the blade, stipels 1–2 and glandular knob absent adaxially at petiole apex; typically growing in montane rainforest (580–)1280–2440 m. 4
4. Fruits 2.8–3.7 cm in diam, seeds “large,” 19.2–19.6 × 17–18.5 × 13–15.7 mm; distributed in central and southern Peru (Cusco, Junín, Pasco). 24. *P. sylvestris*
4. Fruits 4–10 cm in diam, seeds “extra-large,” 27–50 × 25–40 × 15–35 mm; distributed in northern Peru (Amazonas, Cajamarca). 5
5. Filaments 0.5–1 (perhaps to ~1.8, see species discussion) mm long; stamens 25–35; staminate cymules densely packed on inflorescence, axis not clearly visible. 19. *P. carolis-vegae*
5. Filaments ~0.5 mm long; stamens 10–15; staminate cymules loosely packed on inflorescence, axis clearly visible. 20. *P. huayllabambana*
3. Interstaminal nectaries slender-cylindrical or ligulate (strap-shaped); leaves: lateral primary veins arching towards the apex $\geq 1/2$ the length of the blade, stipels absent and glandular knob 1 adaxially at petiole apex; growing in lowland to pre-montane rainforest 0–1000 m (montane rainforest to 2100 m in *P. lehmanniana*). 6
6. Styles 20–40% connate, column 3–6 mm long, free style arms 3–6 mm long; fruits squarish in profile; distributed north and west of the Andes in the Pacific coastal and montane regions of Colombia and Ecuador. 21. *P. lehmanniana*
6. Styles 70–95% connate, column 3–14 mm long, free style arms 1–2.5(3) mm long; fruits ovoid in profile; distributed south and east of the Andes in the Amazon basin, the Guianas, and eastern Venezuela, or in southern Mexico. 7
7. Seeds broadly lenticular, “large” to “extra-large,” 24–27 × 21–27 × 14–16 mm; fruits capsules 5.8–7 cm in diam, at least semi-dehiscent; styles 12–14 mm long; distributed in southern Mexico. 18. *P. carabiasiae*
7. Seeds ovoid, “maximum” sized, 49–56 × 33–37 × 30–36 mm; fruits fleshy berries, 5–11 cm in diam, indehiscent; styles 3–8 mm long; distributed in the northern Amazon basin, the Guianas, and eastern Venezuela. 22. *P. polyadenia*

18. *PLUKENETIA CARABIASIAE* J. Jiménez Ram., *Anales Inst. Biol. Univ. Nac. Autón. México, Bot.* 64 (2): 55. 1993. TYPE: MEXICO. Oaxaca: Distrito Tuxtepec, Municipio San Felipe Usila, Cerretera de Arroyo Tambor a Cerro Verde, [17.833°, -96.467°], 500 m, 9 April 1992, *J. Ismael Calzada 17733* (holotype: FCME; isotype: MEXU).

Notes—See Jiménez Ramírez (1993) for species description. This species was described after Gillespie (1993) and is known only from a few collections from the Tuxtepec district of Oaxaca, Mexico (*J. Ismael Calzada 16965* FCME, 17733 FCME, MEXU; *Meave et al. 1550* MO! [accession 04786568, barcode MO-1147591], MO! [accession 6030707, barcode MO-2056000]). It appears to be morphologically similar to *P. polyadenia* but with smaller, at least semi-dehiscent fruit, “large” to “extra-large” broadly lenticular seeds, and longer styles. The staminate floral morphology of *P. carabiasiae* is not yet known.

19. *PLUKENETIA CAROLIS-VEGAE* Bussmann, Paniagua & C. Téllez, *Econ. Bot.* 67 (4): 388. 2013. TYPE: PERU. Amazonas: Provincia de Rodríguez de Mendoza, Distrito de Limabamba, finca of Sr. Rodríguez in Monte Alegre, [-6.58547°, -77.53214°], 1854 m, 19 August 2012, *R.W. Bussmann, N. Paniagua Zambrana, C. Vega Ocaña & R. Arista Melendez 17132* (holotype: HAO (not seen); isotypes: MO [sheet 1 of 2; accession 6605775, barcode MO-2822725; image!], MO [sheet 2 of 2; accession 6605774, barcode MO-2822724; image!]; INBIAPERU [Instituto para el Desarrollo Local Sostenible y la Conservación Biológica y Cultural Andino-Amazónica, Trujillo]). [The two isotype sheets at MO could not be found at the time of writing. They are mistakenly labeled as holotypes according to images on Tropicos.org.]

Discussion—Together, *P. carolis-vegae*, *P. ×huayllabambana*, and our proposed new species *P. sylvestris*, form a high elevation species complex sister to *P. volubilis*. Members of the species complex grow in high elevation montane rainforest in the Andes, 1280–2440 m, and possess staminate flowers with large irregularly shaped interstaminal nectary segments, short styles partly connate into a squarish-cylindrical column usually < 10 mm long, fruits ~3–10 cm in diam with “large” or “extra-large” seeds, and 1–2 thick stipels at their petiole apex.

The two previously described species, *P. carolis-vegae* and *P. ×huayllabambana*, are geographically and morphologically similar to each other. Both taxa are primarily distributed in the Rodríguez de Mendoza Province in northern Peru (Fig. 6), have large fruits 4–10 cm in diam with “extra-large” seeds, and appear to be fully or semi-domesticated with possible cultivation or reintroduction into forests adjacent to farmland. *Plukenetia carolis-vegae* differs by having 25–35 stamens with longer filaments, 0.5–1 mm long (perhaps as long as ~1.8 mm, see below), 4 (rarely 5) staminate sepals, and inflorescences densely packed with staminate cymules. By comparison, *P. ×huayllabambana* has 10–15 stamens with shorter filaments, 0.1–0.3 mm long in its type description (Bussmann et al. 2009) but ~0.5 mm long in an independently measured specimen (*Quipuscoa 381* MO), 5 (rarely 4) staminate sepals, and inflorescences loosely packed with staminate cymules.

We hypothesize that *P. carolis-vegae* is a cultivated species derived from natural populations of our new species *P. sylvestris*. Presently, *P. carolis-vegae* is only known from its type collection (Bussmann et al. 17132), which was collected

from a farmer’s field (Bussmann et al. 2013). It is most clearly distinguished from *P. sylvestris* by its larger fruits and seeds but otherwise they appear to share the densely packed inflorescences and longer filaments that distinguish both species from *P. ×huayllabambana* (based only on illustrations and photographs from Bussmann et al. 2013; no specimens were available for examination). Based on its description, *P. carolis-vegae* also differs by having 25–35 stamens and 4 (rarely 5) staminate sepals, compared to 10–18 stamens and regularly 4–5 staminate sepals in *P. sylvestris*.

Unfortunately, the MO isotype sheets of *P. carolis-vegae* could not be located at the time of writing, but are needed to conduct better morphological comparisons with *P. sylvestris* and to review discrepancies with its species description. For instance, the description of *P. carolis-vegae* characterized its filaments as relatively short, 0.5–1 mm long, and its staminate flowers as lacking nectaries, but the type illustration (Bussmann et al. 2013, Fig. 1C) suggests its filaments can be as long as ~1.8 mm and that large irregularly shaped nectary segments are present. Additionally, its stamens were reported as “25–35 × 0.1–0.3 mm in diameter,” which by convention implies a length of 2.5–3.5 cm, surpassing any stamen length observed in *Plukenetia*. However, Bussmann et al. (2013) also specify that the filaments are 0.5–1 mm long, suggesting there was a typographical error and that 25–35 refers to stamen number and not length. Indeed, the species description of *P. ×huayllabambana* (Bussmann et al. 2009) uses a similar, although less conventional, format (“stamens 10–14, 0.2–0.4 mm in diameter; filaments flattened, broad, 0.1–0.3 mm long”), which suggests the authors intended to report 25–35 stamens.

Distribution, Habitat, and Phenology—Presently, this species is only known from its type collection from the Amazonas region of northern Peru (Fig. 6). It is a twining liana 4–6 m long, found in cultivation at 1855 m elevation. The type collection contains both flowers and fruits and was collected in August.

20. *PLUKENETIA ×HUAYLLABAMBANA* Bussmann, C. Téllez & A. Glenn, *Nordic J. Bot.* 27 (4): 313. 2009. TYPE: PERU. Región Amazonas: Provincia de Rodríguez de Mendoza, El Cedro-Cruzpata, [-6.404°, -77.449°], 1676 m, 5 July 2008, *C. Téllez, C. Vega & L. Cabrera 02* (holotype: INBIAPERU [Instituto para el Desarrollo Local Sostenible y la Conservación Biológica y Cultural Andino-Amazónica, Trujillo]; isotype: K [barcode K001089689; image!]). [The isotype was originally published as housed at MO (Bussmann et al. 2009), but only one sheet of a different collection (*Téllez et al. 004*, MO! [accession 6116702, barcode MO-2255093]) incorrectly labeled as an isotype could be found. The isotype has since resurfaced at Kew (*Téllez et al. 02*, K [barcode K001089689; image!]) and it appears to be the isotype that was originally deposited at MO (“Ex Herbarium” MO [accession 6116701]).]

Discussion—*Plukenetia ×huayllabambana*, along with *P. carolis-vegae* and *P. sylvestris*, form a high elevation species complex sister to *P. volubilis*. Members of the species complex grow in high elevation montane rainforest in the Andes, 1280–2440 m, and possess staminate flowers with large irregularly shaped interstaminal nectary segments, short styles partly connate into a cylindrical column usually < 10 mm long, and 1–2 thick stipels at their petiole apex. Members of the species complex also have larger fruits and seeds, fruits 4–10 cm in diam with “extra-large” seeds in *P. ×huayllabambana* and

P. carolis-vegae, and fruits 2.8–3.7 cm in diam with “large” seeds in *P. sylvestris* (similar in size to *P. volubilis* but with larger seed volume; Cardinal-McTeague et al. 2019a).

This species is a putative hybrid between *P. sylvestris* × *P. volubilis*, which is supported by the presence of a *P. volubilis* plastid genome in accessions of *P. ×huayllabambana* (Cardinal-McTeague et al. 2019a, Fig. S3) and their intermediate staminate floral morphology. Both *P. ×huayllabambana* and *P. volubilis* have stamens with short filaments, ~0.5 mm long, compared to longer filaments, ~0.5–1.4 mm long, in *P. sylvestris*. Staminate sepal number also appears to differ, more frequently with 5 (rarely 4) sepals in *P. ×huayllabambana* and, regularly varying from 4–5 sepals in *P. sylvestris*, and with 4 sepals in *P. volubilis*.

Plukenetia ×huayllabambana is distributed in the Amazonas and Cajamarca Regions of northern Peru (Fig. 6). It is known from only a few collections across three districts but is possibly more common in cultivation. Its staminate flowers were originally described as having filaments 0.1–0.3 mm long and [nectary] disc absent (Bussmann et al. 2009), but our observations found filaments ~0.5 mm long and large irregularly shaped interstaminal nectary segments to be present (*Quipuscoa* 381 MO). The original type illustration shows an immature staminate flower dissected from a bud, whereas the staminate flower at anthesis is aberrant and likely from a non-euphorb species (Bussmann et al. 2009, Figs. 1J and 1H, respectively).

Specimens Examined—Peru. —AMAZONAS: Chachapoyas District, Distrito Leymebamba [sic], Los Chichos/San Lucas, [−6.701°, −77.586°], 2150 m, 19 June 2000, *Gruhn et al.* 84 (MO [accession 6406258, barcode MO-2695407; seeds: accession 5451714, barcode MO-2695406]); Rodríguez de Mendoza District, Michina, [−6.378°, −77.527°], 1608 m, 5 June 2008, *Téllez et al.* 004 (MO [accession 6116702, barcode MO-2255093]); Rodríguez de Mendoza District, Quebrada Seca, [−6.378°, −77.527°], 1608 m, 5 June 2008, *Téllez et al.* 006 (NY [barcode 02200737; image!]). —CAJAMARCA: San Ignacio, Distrito San José de Lourdes, Villarrica, Nororiental del Marañón RENOM, [−4.917°, −78.833°], 1200–1420 m, 28 October 1995, *Quipuscoa* 381 (MO [5294603, barcode MO-302027]).

21. *PLUKENETIA LEHMANNIANA* (Pax & K.Hoffm.) Huft & L.J. Gillespie, *Syst. Bot.* 18 (4): 584. 1993. *Eleutherostigma lehmanniana* Pax & K.Hoffm. in A.Engler (ed.), *Pflanzenr.* IV, 147, IX (Heft 68): 11, t.3. 1919. TYPE: COLOMBIA. Nariño, Ricaurte, 1000–1400 m, *F.C. Lehmann* 5158 (holotype: B [destroyed]; lectotype designated by Gillespie 1993: K! [barcode K000600748]; isolectotype: K! [barcode K000600749]).

Plukenetia chaponensis Croizat, *Caldasia* 2: 431. 1944. TYPE: COLOMBIA. Boyaca, region of Mt. Chapón, 3600 ft [1097 m], 29 June 1932, *A.E. Laurant* 276 (holotype: A! [barcode 00048691]; isotypes: BM!, F [accession 707024, barcode V0057061F; image!], F [accession 1499186, barcode V0057062F; image!], K! [barcode K000600750], MO!, NY! [barcode 00579365], SI, US! [accession 1482565, barcode 00386091]).

Notes—See Gillespie (1993) for species discussion.

22. *PLUKENETIA POLYADENIA* Müll.Arg. in Martius (ed.), *Fl. Bras.* 11 (2): 334. 1874. *Elaeophora polyadenia* (Müll.Arg.) Ducke, *Arch. Jard. Bot. Rio de Janeiro* 5: 146. 1930. TYPE: PERU. Maynas, *E.F. Poeppig* 2385 (lectotype designated here: G! [barcode G00441993]; isolectotypes: F! [fragment], W [photo at F!]; likely isolectotypes (mislabelled as *E.F. Poeppig* 2585): HAL [barcode HAL0140191; image!], NY! [barcode 00273181]).

Elaeophora abutifolia Ducke, *Arch. Jard. Bot. Rio de Janeiro* 4: 112. 1925. *Plukenetia abutifolia* (Ducke) Pax & K.Hoffm. in

Engler & Prantl (eds.), *Nat. Pflanzenfam.*, ed. 2, 19c: 141. 1931. TYPE: BRAZIL. Pará: Breves Antonio Lemos, margem inundada do Rio Tajapurú, 5 May 1923, *A. Ducke s.n.* (lectotype designated here: RB [accession 17893, barcode 00283479; image!]; isolectotypes: G [barcode G00441992; image!], IAN [accession 50621, barcode IAN05061; image!], K [barcode K000600770; image!], P! [barcode P00645482], S [barcode S-R-10641; image!], U [barcode U 0002066; image!], US [accession 1442272, barcode 01105949; image!]).

Notes—See Gillespie (1993) for species discussion and Gillespie and Armbruster (1997) for species description.

There is sufficient ambiguity over the type of *P. polyadenia* to warrant designating a lectotype. The specimen at G, where Müller worked, is limited to a single leaf and inflorescence fragment, suggesting the detailed type description was based on additional material. Three specimens of *E.F. Poeppig* 2385 reported on the Vienna Virtual Herbarium (<https://herbarium.univie.ac.at>; last accessed 28 November 2019) are likely candidates given that Poeppig’s types are often housed at W (Stafleu and Cowan 1983), however at the time of writing we were unable to access the specimens to make an assessment. In this situation, we designate a lectotype based on the only specimen that we were able to verify, housed at G.

Of the three syntypes cited in the protologue of *Elaeophora abutifolia*, *A. Ducke s.n.*, RB 17893 has the best floral material. Overall, the U specimen (now housed at L) most clearly demonstrates the pistillate morphology, but by convention we lectotypify the original syntype housed in Ducke’s herbarium at the Jardim Botânico do Rio de Janeiro. Remaining syntypes: BRAZIL. Pará: Belém Marutucui, capoeira úmida, 18 October 1923, *A. Ducke s.n.* (RB [accession 17892, barcode 00283480; image!]); SaPo Felix do Xingu Estrada da Victoirio ao Forte, 21 April 1924, *J.G. Kuhlmann* 2051 (RB [accession 17895, barcode 00724931; image!], RB [barcode 00287343; image!], S [accession S-R-10855; image!], U! [barcode U 0002067]).

23. *PLUKENETIA STIPELLATA* L.J.Gillespie, *Syst. Bot.* 18 (4): 588. 1993. TYPE: COSTA RICA. Heredia: Finca La Selva, OTS Field Station on the Río Puerto Viejo, just E of junction with the Río Sarapiquí, [10.400°, −84.000°], 100 m, 13 September 1983, *L.J. Gillespie* 413 (holotype: US! [accession 3274018, barcode 00432786]; isotypes: CR!, MO!, NY! [barcode 00022625]; FAA preserved material at US!).

Notes—See Gillespie (1993) for species description.

24. *Plukenetia sylvestris* Card.-McTeag. & L.J.Gillespie sp. nov. TYPE: PERU. Cusco. La Convención, Dist. Ocobamba, Versalles, Santa Elena, 1942 m, [−12.78333°, −72.30527°], 24 November 2007, *L. Valenzuela, Ciro Astete, F. Zamora, N. Suares & M. Atausupa* 10453 (holotype: CAN!; isotypes: CUZ, MO!).

Similar to *Plukenetia carolis-vegae* Bussmann, Paniagua & C.Téllez but with smaller fruits and seeds and found in natural/non-cultivated populations from central and southern Peru.

Description—Monoecious lianas; stems erect or twining; older stems dull olive green to brown when dry, to 10 mm in diam, striate, sparsely to moderately puberulous (pubescent); younger stems striate, sparsely puberulous to pubescent. **Leaves** alternate, evergreen; stipules (narrowly) broadly triangular to deltoid, 0.4–1.5(–2) mm long, persistent but frequently stretched or broken in older stems; petioles 2–7.4 cm

long, glabrate to puberulous; blades simple, moderately to broadly ovate (orbicular), $6.5\text{--}13.5 \times 4.3\text{--}11$ cm, chartaceous, both surfaces glabrate to puberulous, typically hairier (to pubescent) on major and minor veins, base cuneate, truncate, or rounded (subcordate), margins minutely serrulate (subcrenulate) with small glandular teeth, apex acuminate, tip

$0.5\text{--}1.5$ cm long; venation palmate, primary veins 3, secondary veins 2–4 on each side of the midrib, weakly brochidodromous, tertiary veins percurrent; stipels 1–2 at petiole apex, ligulate or knobby, $0.5\text{--}1$ mm long; adaxial basilaminar extrafloral nectaries 2, narrowly to broadly elliptic (obovate), typically straddling the margin, $1.3\text{--}3.3 \times 0.2\text{--}1.2$ mm; laminar

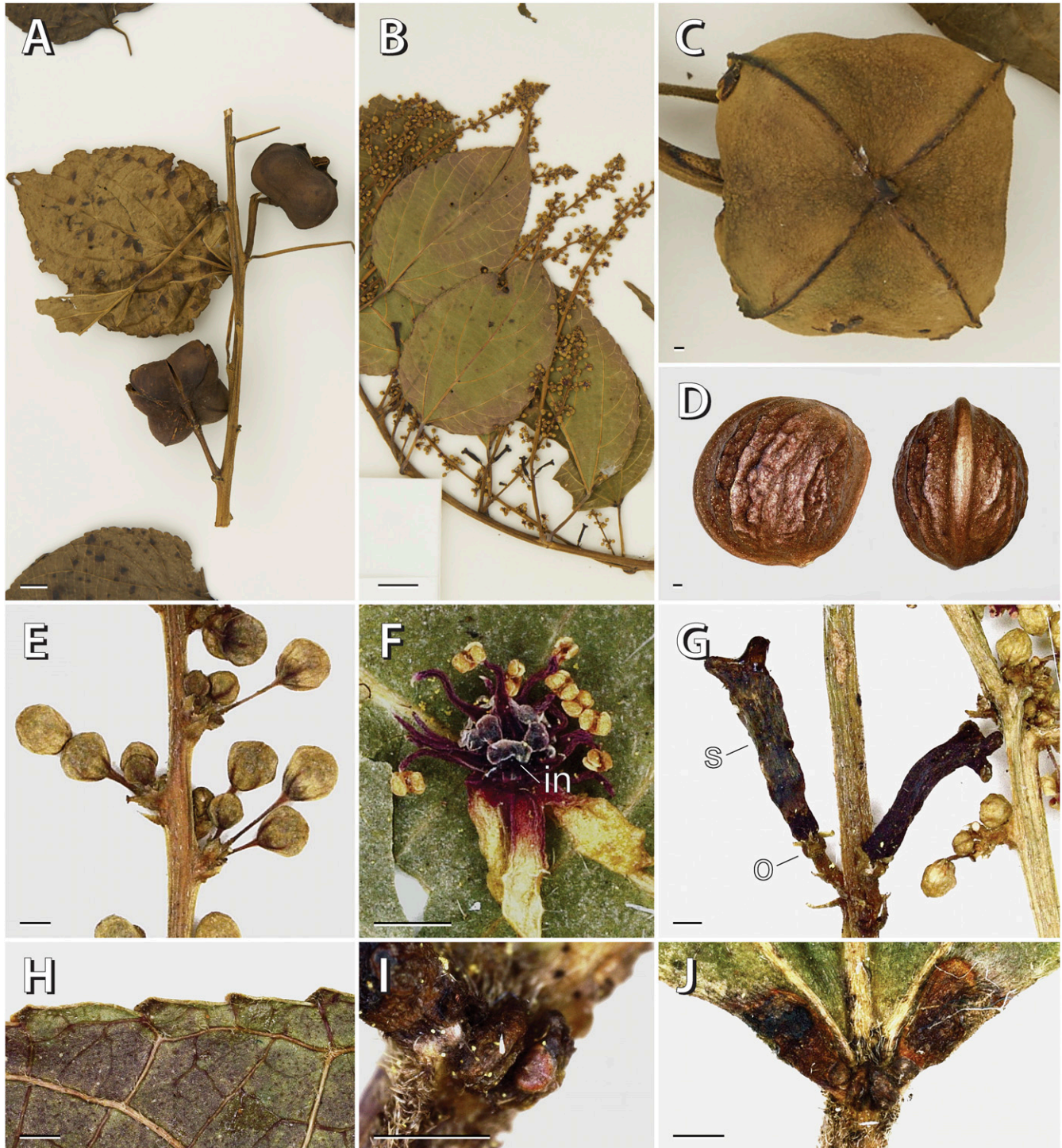


FIG. 9. *Plukenetia sylvestris* sp. nov. A. Branch with mature dehiscent fruit. B. Branch with mature leaves and inflorescences. C. Capsule. D. Seed, lateral view (left), dorsal view (right). E. Close-up of staminate cymules. F. Staminate flower. G. Pistillate flowers. H. Abaxial leaf blade with minutely serrulate margins with small glandular teeth. I. Pair of thick stipels. J. Adaxial leaf blade with basilaminar extrafloral nectaries and pair of thick stipels. Photos by W. Cardinal-McTeague. Source: A. Valenzuela et al. 10453 (CAN); B, E–J. Woytkowski 6670 (MO); C. Farfán et al. 1820 (CAN); D. Ortiz et al. 191 (CAN). (Abbreviations: in = interstaminal nectaries; o = ovary; s = style. Scale bars: A = 1 cm; B–I = 1 mm).

extrafloral nectaries absent. **Inflorescences** axillary, bisexual racemose thyrses (appearing unisexual if pistillate flowers or staminate axis dropped), 3–14.5 cm long (2–3 cm if staminate axis dropped), 1(2)/axil; peduncle 3.3–25 mm long; axis sparsely puberulous to pubescent; staminate bracts triangular to ovate, 0.5–1.5 mm long, glabrate to puberulous along the margins, bracteoles similar or smaller; pistillate bracts narrowly triangular to deltoid, 0.8–1.4 mm long, glabrate to puberulous along the margins, bracteoles similar or smaller; staminate flowers numerous, distal, 3–15(–18)/node in condensed cymules (thick cyme axes apparent in mature cymules); pistillate flowers 1–4, basal, 1/node (frequently dropped or partly dropped when staminate flowers are at anthesis). **Staminate flowers:** pedicel 2–7.5 mm long at anthesis, glabrous; buds ovoid to obovoid, apex obtuse to rounded; sepals 4–5, reflexed or spreading at anthesis, lanceolate to ovate, 1.5–3 × 0.5–1.2 mm, apex acute, glabrous; receptacle globose, mostly covered with stamens and nectaries; nectaries of large irregularly shaped segments intermixed between stamens; androecium subglobose and convex, 0.2–1 × 0.6–1.2 mm, stamens 10–18, filaments slender cylindrical, 0.7–1.4 mm long, anthers dorsifixed, anther sacs ellipsoid, dehiscing longitudinally. **Pistillate flowers:** pedicel (comprising cyme axis and true pedicel) 1–3.2 mm long, glabrate to puberulous; sepals 4, narrowly to moderately triangular, 0.8–1.4 × 0.3–0.6 mm, glabrate; ovary 4-lobed, 0.5–1.8 × 0.7–1.4 mm, lobes rounded and laterally compressed, glabrous to glabrate, conspicuous wings or horns absent; styles 4, partly connate into a squarish column with free style arms spreading at the apex, entire length 5.2–11.5 mm, column width 0.8–1.2 mm, apex width 0.9–4.5 mm, 4-lobed distally, glabrate; free style arms 4, obtuse or spreading (erect), unlobed or slightly 2-fid, 0.8–1.8 mm long; stigmas 4, 0.5–1.3 mm wide, smooth to microverrucose (short-papillose); flowers developing into fruit similar but larger. **Fruits** a 4-lobed capsule, squarish in cross-section, 1.9–3.5 × 2.9–3.7 cm, surface dull brown, microverrucose (large irregular verrucae), glabrate, each carpel lobe subglobose and slightly laterally compressed, carinate, keels 0.5–1.8 mm long; stylar columns persistent or not; pedicel (comprising cyme axis and true pedicel) 7–20 mm long. **Seeds** broadly lenticular, laterally compressed, elliptic to subcircular in outline, 17–19.3 × 17.5–18.5 × 13.4–15.9 mm, ventral surface moderately to obtusely angular, dorsal surface rounded with a radial ridge, dull light brown to yellowish dark brown, with irregular shallow ridges and reticulations; testa persistent. Figure 9.

Etymology—The specific epithet is Latin (of the forest), referring to the primary or secondary montane forest where this species is found. It also means wild, which is fitting since we consider *P. sylvestris* the wild progenitor of the cultivated species *P. carolis-vegae*.

Distribution, Habitat, and Phenology—This species is known from two disjunct populations from central (Junín and Pasco) and southern (Cusco) regions of Peru (Fig. 6). They are twining vines and lianas climbing to 10 m in primary and secondary montane forest, sometimes partly disturbed and along roadsides, forest edges, or riparian forest, at (580–) 1280–2440 m elevation. Flowering specimens were collected in February, March and May through September, fruiting specimens from September through February.

Discussion—*Plukenetia sylvestris* is morphologically similar to *P. carolis-vegae* but differs by its smaller fruits and seeds (fruits 2.8–3.7 cm in diam and seeds “large” in *P. sylvestris* compared to fruits 6–10 cm in diam and seeds “extra-large” in *P. carolis-vegae*)

and stamen number (10–18 in *P. sylvestris* compared to 25–35 in *P. carolis-vegae*; based on species description only, type material of *P. carolis-vegae* was not available). They also differ in their geographic distribution (Fig. 6), with *P. sylvestris* being widespread in central and southern Peru and found in natural habitats and *P. carolis-vegae* being narrowly distributed in northern Peru and so far only known from its type collection in cultivation. A previous molecular phylogeny based on two plastid (*matK*, *ndhF*) and five nuclear (ETS, ITS, *KEA1* introns 11 and 17, *TEB* exon 17) markers resolved *P. sylvestris* (referred to as *P. cf. carolis-vegae*) in a strongly supported clade sister to *P. volubilis* (Cardinal-McTeague et al. 2019a; summarized in Fig. 1). The putative hybrid species *P. ×huayllabambana* is thought to have resulted from a cross between *P. sylvestris* × *P. volubilis*, supported by the introgression of a *P. volubilis* plastid genome in *P. ×huayllabambana* (which otherwise has the nDNA of *P. sylvestris*; Cardinal-McTeague et al. 2019a, Fig. S3) in addition to their intermediate staminate flowers (see discussion of *P. ×huayllabambana*). Together, *P. carolis-vegae*, *P. ×huayllabambana*, and *P. sylvestris* form a high elevation species complex sister to *P. volubilis*, united by their habitat preference (Andean montane rainforest, 1280–2440 m), floral morphology (staminate flowers with large irregularly shaped interstaminal nectary segments, pistillate flowers with short styles partly connate into a squarish-cylindrical column usually < 10 mm long), typically larger fruits and seeds (fruits 4–10 cm in diam with “extra-large” seeds in *P. carolis-vegae* and *P. ×huayllabambana*; fruits 2.8–3.7 cm in diam with “large” seeds in *P. sylvestris*), and the presence of 1–2 thick stipels at their petiole apex.

The collection Woytkowski 6670 exhibits well preserved floral material (e.g. Fig. 9) but is unusual for having two inflorescences per leaf axis (versus one) and for having basilar extrafloral nectaries that are predominantly on the adaxial surface (versus straddling the blade margin).

Specimens Examined—Peru. —CUSCO: La Convención, Dist. Santa Ana, Poromate, [-12.917°, -72.783°], 2118 m, 16 June 2003, Calatayud et al. 1470 (CAN, MO); La Convención, Dist. Vilcabamba, Espiritupampa, [-12.914°, -72.212°], 1544 m, 23 July 2004, Calatayud et al. 2643 (CAN, MO); La Convención, Dist. Santa Ana, Tunquimayo, [-12.909°, -72.813°], 2110 m, 20 September 2004, Calatayud et al. 2746 (CUZ, MO [accession 4837341, barcode MO-1102090; accession 04837342, barcode MO-1102089]); La Convención, Distrito Santa Ana, Localidad Tunquimayo, [-12.907°, -72.821°], 2007 m, 19 October 2007, Farfán et al. 1820 (CAN, MO); La Convención, Dist. Echarati, Monte Cristo, [-13.5°, -72.317°], 1447 m, 29 July 2005, Huamantupa et al. 6445 (CAN, MO); Ca. 5 km N of Aguas Calientes (km. 116 on railroad), ca. 2000 m, 7 June 1977, Solomon 3166 (MO [accession 2637789, barcode MO-1381661]); La Convención, Dist. Occobamba, Santa Elena, [-12.45°, -72.167°], 1995 m, 24 February 2005, Valenzuela et al. 5197 (CAN, MO); La Convención, Dist. Santa Ana, Bosque del Chuyapi, [-12.949°, -72.785°], 2100 m, 19 July 2006, Valenzuela et al. 7297 (CAN, MO); La Convención, Distrito Santa Ana, Tunqui Mayo, [-12.901°, -72.762°], 1870 m, 2 November 2007, Vasquez et al. 33145 (MO). —JUNÍN: Yaupi, dept. Junín, 1600 m, 19 July 1961, Woytkowski 6670 (MO [accession 2154072, barcode MO-1381660]). —PASCO: Oxapampa, Distrito Huancabamba, Zona de Amortiguamiento del Parque Nacional Yanachaga-Chemillén, sector Tunqui, [-10.287°, -75.523°], 1753 m, 13 September 2007, Castillo et al. 965 (CAN, MO); Cordillera Yanachaga, E of Oxapampa, lumber road to Chacas microwave station, 10 km E of main road, [-10.583°, -75.25°], 2040–2110 m, 2 March 1982, Gentry & Smith 35906 (MO [accession 2983786, barcode MO-1381639]); Oxapampa, Distrito Oxapampa, Parte alta de la quebrada San Luis, [-10.565°, -75.345°], 2440 m, 30 May 2007, Monteagudo et al. 14125 (CAN, MO); Oxapampa, Distrito Huancabamba, Parque Nacional Yanachaga-Chemillén, Sector Tunqui, [-10.289°, -75.518°], 1790 m, 22 September 2007, Monteagudo et al. 15253 (CAN, MO); Oxapampa, Dist. Villa Rica, Palma Centro Bocaz, camino a Alto Atarraz-Zona de Amortiguamiento, Parque Nacional Tanachaga-Chemillén, [-10.65°, -75.193°], 1515 m, 14 January 2005, Ortiz et al. 191 (CAN, MO); Oxapampa, Distrito Villa Rica, Localidad Centro Bocaz, [-10.633°, -75.167°], 1280 m, 17 September 2003, Perea et al. 282 (CAN, MO); Oxapampa, Dist. Oxapampa, Abra Villa Rica, [-10.4°, -75.183°], 2000 m, 26 August 2005, Rojas et al. 3863 (CAN, MO);

Oxapampa, Distrito Pozuzo, Camino de Puente Victoria hacia la Comunidad Nativa Alto Lagarto, [-10.1°, -75.433°], 700 m, 29 September 2007, *Rojas et al.* 4648 (MO [accession 6126857, barcode MO-2131172], USM); Oxapampa, Dist. Palcazú, Comunidad Nativa de Alto Lagarto, [-10.199°, -75.356°], 700 m, 3 December 2007, *Rojas et al.* 4827 (CAN, MO); Oxapampa, Dist. Pozuzo, Alto Lagarto a Puente Victoria, [-10.1°, -75.433°], 700 m, 28 December 2007, *Rojas & Ortiz* 5152 (CAN, MO); Oxapampa, Dist. Palcazú, Comunidad nativa Alto Lagarto - Reserva Comunal Yanasha., [-10.152°, -75.392°], 584 m, 30 October 2009, *Rojas & Ortiz* 7102 (CAN, MO); Oxapampa, Road from Oxapampa to San Alberto, [-10.533°, -75.35°], 2250 m, 20 June 2003, *van der Werff et al.* 17532 (CAN, MO); Oxapampa, Along old road Oxapampa-Villa Rica, [-10.633°, -75.367°], 2000 m, 25 June 2003, *van der Werff et al.* 17759 (CAN, MO), 17760 (CAN, MO); Oxapampa, Distrito Bermudez, Bosque Protección San Matias-San Carlos, Sector Unión-Shimaki, [-10.75°, -74.917°], 1382 m, 12 February 2003, *Vasquez et al.* 27906 (HUT, MO [accession 5709828, barcode MO-300971], USM).

25. *PLUKENETIA VOLUBILIS* L., Sp. Pl. 1 (2): 1192. 1753. *Sajorium volubile* (L.) Baill., Étude Euphorb. 483. 1858. TYPE: WEST INDIES. Illustration t.13 (lower half) in Plumier, Nov. Pl. Amer. 1703 (lectotype designated by Howard 1989).

Plukenetia peruviana Müll.Arg., Linnaea 34: 157. 1865. TYPE: PERU. Peruvia, Herb. Pavon [likely *H. Ruiz & J. Pavón s.n.*] (lectotype designated here: G! [barcode G00418846]; isolectotype: G-DC! [barcode G00313656; photo at F!]).

Plukenetia macrostyla Ule, Verh. Bot. Vereins Prov. Brandenburg 50: 80. 1908. TYPE: BRAZIL. Amazonas: Rio Juruá sup., September 1901, *E. Ule* 5864 (holotype: B [destroyed]; lectotype designated here: G! [barcode G00441991; photo at F!]; isolectotypes: F! [fragment], HBG [barcode HBG-515849; image!], MG [barcode MG005766; image!]).

?*Fragariopsis paxii* Pittier, J. Wash. Acad. Sci. 19: 351. 1929. TYPE: VENEZUELA. Aragua: Hacienda Puerto La Cruz, Coastal Range, 1000 m, 28 August–4 September 1918, *H. Pittier* 8109 (holotype: VEN [accession 6906, barcode VEN 6906; image!]; isotype: GH! [barcode 00048014], US! [accession 988210, barcode 00096452]). [appears to be intermediate between *P. stipellata* and *P. volubilis*; see discussion of Gillespie 1993 for more detail]

Notes—See Gillespie (1993) for species discussion and Gillespie and Armbruster (1997) for species description.

Taxonomic Discussion—The *P. volubilis* species complex includes a main group of typical lowland moist to wet forest *P. volubilis*, plus two smaller groups that differ in morphology and phylogeny and may warrant their own taxonomic rank. The first is an open savanna species group found on the Moxos Plains of Bolivia. This group has broad leaf blades with subcordate bases similar to the typical moist or wet forest *P. volubilis*, but differs in its habitat, generally thicker leaf blades, and smaller seeds/fruit (“medium” compared to “large” sensu Cardinal-McTeague et al. 2019a). Accessions of the open savanna group (known only from *Nee* 55162 MO and *Parada et al.* 206 CAN, MO) form a strongly supported clade sister to the remaining moist to wet forest *P. volubilis* (Cardinal-McTeague et al. 2019a), suggesting this group could represent a distinct taxon on the basis of ecology and phylogeny. Floral morphology of the open savanna group is not yet known and additional collections are needed to verify if there are sufficient characters to warrant a new species.

The second is a mid-elevation species group from the Andes of Bolivia and Peru. Individuals in this group are found at higher elevations, (200)500–900(1800) m, than the typical moist to wet forest species group (usually to 500 m). The mid-elevation group is known from many collections across

Bolivia (*Jaramillo et al.* 1237 MO [208 m]; *Teran et al.* 2006 MO [800 m]; *Teran et al.* 2502 MO [1800 m]) and Peru (*Foster & Wachter* 7404 MO [500–600 m]; *Gentry et al.* 40071 MO [830–900 m]; *Huamán.* 188 MO [290 m]; *Huamantupa et al.* 3500 MO [780 m]; *Núñez* 13775 MO [640 m]; *Rojas et al.* 4349 MO [800 m], 4593 MO [800 m], 5222 MO [600 m], 5525 MO [1500 m], 5665 MO [600 m], 8491 MO [500 m]; *Rojas & Ortiz* 6726 MO [500 m]; *Valenzuela et al.* 8531 MO [739 m], 9242 MO [1200 m], 10968 MO [1000 m], 12029 MO [375–635 m]; *van der Werff et al.* 18445 MO [700 m]). These collections are differentiated by their narrower leaf blades and cuneate or truncate bases, compared to broader leaf blades with subcordate or cordate bases in typical *P. volubilis*. Other characters such as style length and fruit/seed size share the same breadth of variation observed in the typical *P. volubilis* group. Phylogenetic analyses suggest mid-elevation accessions (*Huamantupa et al.* 3500, *Jaramillo et al.* 1237, *Teran et al.* 2502, *Valenzuela et al.* 8531) form a strongly supported clade embedded within typical *P. volubilis* (Cardinal-McTeague et al. 2019a). Although the mid-elevation group appears to form a cohesive lineage within *P. volubilis*, it exhibits considerable geographical overlap and gradation of leaf shape characters with the typical lowland moist and wet forest group, and might be better recognized as an ecological variant without taxonomic status.

Further work is needed to clarify species group boundaries in the *P. volubilis* complex. Future studies should test the resolution of our proposed groups with improved taxon sampling across the geographic range of *P. volubilis*, specifically from the central and eastern Amazon basin, the Guianas, and the Lesser Antilles. Additionally, the putative hybrid population in Venezuela, intermediate between *P. stipellata* and *P. volubilis* (associated with the tentative synonym ?*Fragariopsis paxii*; see Gillespie 1993), requires further investigation.

Here we designate lectotypes for two of the synonyms of *P. volubilis*. The protologue of *P. peruviana* listed two specimens as syntypes, “In Peruvia (hb. Pavon!)” and “in prov. Maynas (Poeppeg n.2110!)”. We have not yet observed *E.F. Poeppeg* 2110 and at the time of writing the G herbarium could not locate such a specimen (L. Gautier pers. comm.), which precludes its evaluation. Of the Pavon sheets, we select the G00418846 specimen as lectotype since it has abundant floral material as well as a developing fruit. The presumed holotype of *P. macrostyla* was destroyed in Berlin. Although each of its isotypes are in good condition and demonstrate pistillate flower morphology, we designate the G00441991 specimen as lectotype since it also contains staminate buds near anthesis.

ROMANOA Trevis., Sagg. Algh. Coccot. 99. 1848. *Anabaena* A.Juss., Euphorb. Gen. 46, 1824, nom. rej., non. Bory ex Bornet & Flahault 1888. *Sajorium* sect. *Anabaena* (A.Juss.) Baill., Étud. Euphorb. 484. 1858. *Plukenetia* sect. *Anabaena* (A.Juss.) Müll.Arg., Linnaea 34: 158. 1865. *Anabaenella* Pax & K.Hoffm. in A.Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 27. 1919, nom. illeg. TYPE: *Anabaena tamnoides* A.Juss. [= *Romanoa tamnoides* (A.Juss.) Radcl.-Sm.]

Taxonomic Discussion—The genus *Romanoa* Trev. 1848 is the earliest published replacement name for *Anabaena* A.Juss. 1824, nom. rej., after the well-known genus of cyanobacteria, *Anabaena* Bory ex Bornet & Flahault 1888, was conserved. The replacement name *Anabaenella* Pax & K.Hoffm. 1919 was used for much of the 20th century until the lesser-known *Romanoa* was re-discovered by Punt (1962) and nomenclaturally

corrected by Radcliffe-Smith (1980). *Romanoa* was briefly treated as a synonym of *Plukenetia*, first as *Sajorium* sect. *Anabaena* (Baillon 1858) then *Plukenetia* sect. *Anabaena* (Müller 1865), but has often been regarded as a separate genus for having plesiomorphic 3-carpellate ovaries, compared to 4-carpellate in *Plukenetia*. Pollen morphology further supported the recognition of *Romanoa* (Gillespie 1994) and molecular phylogeny suggests they are distinct and form sister genera (Cardinal-McTeague and Gillespie 2016).

1. ROMANOA TAMNOIDES (A. Juss.) Radcl.-Sm., Kew Bull. 34 (3): 589. 1980. *Anabaena tamnoides* A. Juss., Euphorb. Gen. 115, t.15. 1824. *Sajorium tamnoides* (A. Juss.) Baill., Étude. Euphorb. 484. 1858. *Plukenetia tamnoides* (A. Juss.) Müll. Arg., Linnaea 34: 158. 1865. *Anabaenella tamnoides* (A. Juss.) Pax & K. Hoffm. in A. Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 27. 1919. *Anabaenella tamnoides* var. *genuina* Pax & K. Hoffm. in A. Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 27. 1919, nom. illeg. TYPE: BRAZIL. Brésil, 1819, *Leandro di Sacramento s.n.* (lectotype designated here: P [barcode P00645483; image!]).

Croton scandens Vell., Fl. Flumin. Icon. 10: t.72. 1831. TYPE: illustration in t.72.

Plukenetia sinuata Ule, Bot. Jahrb. Syst. 42 (2–3): 217. 1908. *Anabaenella tamnoides* var. *sinuata* (Ule) Pax & K. Hoffm. in A. Engler (ed.), Pflanzenr. IV, 147, IX (Heft 68): 27. 1919. *Romanoa tamnoides* var. *sinuata* (Ule) Radcl.-Sm., Kew Bull. 34 (3): 589. 1980. TYPE: BRAZIL. Bahia: Serra do São Ignacio, February 1907, E. Ule 7445 (holotype: B [destroyed]; lectotype designated here: L! [accession 601470, barcode L 0137705]; isolectotype: HBG [barcode HBG-515848; image!]).

Notes—Historically, *Romanoa tamnoides* was thought to be endemic to the Atlantic Forest region of Brazil and Paraguay (Pax and Hoffmann 1919), but it has since been collected in Bolivia (Jorgensen et al. 2014). This species has been poorly studied and a revised treatment across its expanded range seems warranted.

Taxonomic Discussion—Originally, two syntypes were designated for *Anabaena tamnoides*, “Species unica brasiliensis (in Herb. Mus. et J.)” (Jussieu 1824, p. 47), which refer to *Leandro di Sacramento s.n.* (P0064583) and *herb. Dombey s.n.* (P00678933). Radcliffe-Smith (1980) inaccurately cited *Dombey s.n.* as the holotype of *A. tamnoides*, which did not qualify as a valid lectotype designation. Both sheets are relatively poor in quality, *herb. Dombey s.n.* with better preserved leaves and a 3-carpellate fruit, and *Leandro di Sacramento s.n.* with degraded leaves but more abundant floral material, including intact stylar columns. We select *Leandro di Sacramento s.n.* as the lectotype since it demonstrates the distinctive pistillate floral morphology of the species and genus. Remaining syntype: BRAZIL. Breisil, *herb. Dombey s.n.* (P-JU [barcode P00678933; image!]).

Both syntypes of *Anabaena tamnoides* were annotated as “*Plukenetia occidentalis*” Leandro (in mss.). Jussieu (1824) and Baillon (1858) listed *P. occidentalis* as a synonym of *A. tamnoides*; however, neither case resulted in valid publication of that name (ICN 2017, Art. 36.1; Turland et al. 2018).

Lastly, we designate a lectotype for *P. sinuata* since the presumed holotype was destroyed in Berlin. Both isotypes have abundant floral material, but our selected lectotype (L0137705) also includes fruit.

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AUTHOR CONTRIBUTIONS

Both authors conceptualized the study. WCM produced the data, figures, and manuscript text and was the primary author of the sections and most new taxa. LG provided comments, guidance, and mentorship on the genus and study, and was the primary author of *P. choceensis*. Both authors edited and approved the final manuscript.

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APPENDIX 1. List of species and vouchers used in the ETS phylogeny (Fig. 4), arranged by: *Species*. COUNTRY. Collector & Number (Herbarium Code), GenBank accession number. Most sequences are from Cardinal-McTeague

et al. (2019a); a single new ETS sequence is published for *P. brevistyla* Card.-McTeag. & L.J.Gillespie sp. nov., indicated by an asterisk (*).

Ingroup: *Plukenetia africana* Sond. BOTSWANA. *Palomoti* 1086 (MO), MF502432; *Pope et al.* 834 (MO), MF502433. NAMIBIA. *Bartsch* 1859 (US), MF502431. *P. ankaranensis* L.J.Gillespie. MADAGASCAR. *Gillespie* 10697 (CAN), MF502434; *Lees s.n.* (CAN), MF502435. *P. brachybotrya* Müll.Arg. BOLIVIA. *Araujo-M. et al.* 1722 (MO), MF502437; *Fuentes & Torrico* 5398 (MO), MF502438; *Seidel & Vaquiata* 7733 (MO), MF502440. PERU. *Acevedo-Rodriguez* 14416 (NY), MF502436; *Galiano et al.* 6612 (MO), MF502439. *P. brevistyla* Card.-McTeag. & L.J.Gillespie sp. nov. BRAZIL. *Lowrie et al.* 30 (MO), MH119142*. *P. carabiasiae* J.Jiménez Ram. MEXICO. *Meave et al.* 1550 (MO), MF502441. *P. choocoensis* L.J.Gillespie & Card.-McTeag. COLOMBIA. *Gentry* 47799 (MO), MF502442. *P. conophora* Müll.Arg. DEMOCRATIC REPUBLIC OF THE CONGO. *Hart* 1621 (MO), MF502443. CAMEROON. *Nemba & Thomas* 434 (MO), MF502444. *P. corniculata* Sm. BANGLADESH. *Huq & Haroon* 10780 (MO), MF502446. *P. decidua* L.J.Gillespie. MADAGASCAR. *Rakotomalaza* 597 (CAN), MF502447. *P. huayllabambana* Bussmann, C.Téllez & A.Glenn. PERU. *Quipuscoa* 381 (MO), MF502452; *Téllez et al.* 4 (MO), MF502454. *P. lehmanniana* (Pax & K.Hoffm.) Huft & L.J.Gillespie. COLOMBIA. *Silverstone-Sopkin & Giralda-Gesini* 8019 (MO), MF502461. ECUADOR. *Acevedo-Rodriguez & Daly* 1658 (MO), MF502459; *Clark* 3953 (MO), MF502460; *Zak & Jaramillo* 3401 (MO), MF502462. *P. lorentensis* Ule. BOLIVIA. *Solomon* 7972 (MO), MF502466. PERU. *Grandez* 19608 (AMAZ), MF502463; *McDaniel & Rimachi* 22451 (MO), MF502464; *Rimachi* 5122 (MO), MF502465; *Vásquez & Jaramillo* 3283 (MO), MF502467; *Vásquez et al.* 38069 (MO), MF502468. *P. madagascarensis* Leandri. MADAGASCAR. *Andrianjafy* 1648 (CAN), MF502469; *Gillespie* 4175 (CAN), MF502470; *Villiers et al.* 4899 (MO), MF502471. *P. megastyla* Card.-McTeag. & L.J.Gillespie sp. nov. BOLIVIA. *Ledezma et al.* 921 (CAN), MF502428. BRAZIL. *Sperling et al.* 5873 (MO), MF502429; *Sperling et al.* 6161 (CAN), MF502430. *P. penninervia* Müll.Arg. BELIZE. *Atha et al.* 1001 (MO), MF502472. GUATEMALA. *Wallnöfer & Frisch* 5996 (MO), MF502477. MEXICO. *Carnevali & Duno* 7594 (MO),

MF502473; *Martínez* 10527 (MO), MF502474; *Martínez* 17705 (DAV), MF502475. PANAMA. *McPherson* 8461 (MO), MF502476. *P. polyadenia* Müll.Arg. GUYANA. *Wurdack* 5288 (US), MF502479. SMITHSONIAN GREENHOUSE ex FRENCH GUIANA. *Gillespie* 4314 (CAN), MF502478. *P. serrata* (Vell.) L.J.Gillespie. BRAZIL. *Davidse* 10480 (MO), MF502480; *Forzza et al.* 5328 (RB), MF502481; *Goldenberg et al.* 1424 (RB), MF502482; *Peixoto et al.* 4154 (MO), MF502483; *Sartori & Pardo* 11 (RB), MF502484; *Thomas* 10221 (NY), MF502485. *P. stipellata* L.J.Gillespie. COSTA RICA. *Aguilar* 8193 (MO), MF502486; *Cardinal-McTeague* 8 (CAN), MF502487; *Liesner* 3088 (MO), MF502489; *Morales & Rojas* 5342 (MO), MF502490. MEXICO. *Refugio Cedillo Trigas* 3510 (MO), MF502491; *Ibarra Manriquez & Sinaca* 1115 (MO), MF502488. NICARAGUA. *Urbina* 1155 (MO), MF502492. *P. supraglandulosa* L.J.Gillespie. SURINAME. *Acevedo-Rodriguez* 6022 (US), MF502493. *P. sylvestris* Card.-McTeag. & L.J.Gillespie. PERU. *Calatayud et al.* 2643 (CAN), MF502448; *Huamantupa et al.* 6445 (CAN), MF502449; *Monteagudo et al.* 14125 (MO), MF502450; *Monteagudo et al.* 15252 (MO), MF502451; *Rojas et al.* 3863 (CAN), MF502453; *Valenzuela et al.* 5197 (CAN), MF502455; *van der Werff et al.* 17532 (CAN), MF502456; *Vásquez et al.* 33145 (MO), MF502457; *Woytkowski* 6670 (MO), MF502458. *P. verrucosa* Sm. FRENCH GUIANA. *Barrabe & Crozier* 145 (US), MF502494. SURINAME. *Herrera & Kaemar* 10073 (CAN), MF502495; *Hoffman* 5917 (US), MF502496. *P. volubilis* L. BOLIVIA. *Jaramillo et al.* 1237 (MO), MF502501; *Nee* 55162 (MO), MF502502; *Parada et al.* 206 (CAN), MF502503; *Teran et al.* 2502 (MO), MF502504. ECUADOR. *Burnham & Krings* 1640 (MO), MF502498; *Carrillo & Reyes* 448 (MO), MF502499. SMITHSONIAN GREENHOUSE ex PERU. *Wurdack s.n.* (US), MF502506. PERU. *Bell* 93-546 (US), MF502497; *Huamantupa* 3500 (CAN), MF502500; *Valenzuela* 8531 (MO), MF502505.

Outgroup: *Haematostemon guianensis* Sandwith. GUYANA. *Wurdack* 4350 (US), MF502427. *Romanoa tannoides* (A.Juss.) Radcl.-Sm. BOLIVIA. *Fuentes* 1848 (MO), MF502507; *Raes & Terceros* 177 (MO), MF502508; *Raes et al.* 211 (MO), MF502509; PARAGUAY. *Zardini & Chaparro* 50824 (MO), MF502510.