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# A Synopsis of Neotropical *Plukenetia* (Euphorbiaceae) including Two New Species

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ABSTRACT. A synopsis of the eleven neotropical species of *Plukenetia* (Euphorbiaceae) is given. The genus *Plukenetia* is redefined to include the neotropical monotypic genera *Eleutherostigma* and *Vigia* (previously known as *Fragariopsis*). As treated here *Plukenetia* may be distinguished from all other members of the tribe Plukenetieae by its four-carpellate ovary. Two new species, **P. supraglandulosa** from French Guiana and the Brazilian state of Amapá and **P. stipellata** from Mexico and Central America, are described and illustrated. *Plukenetia supraglandulosa* is closely allied with *P. penninervia* and *P. multiglandulosa* and differs in the presence of scattered laminar glands on the upper leaf surface and longer inflorescences. The three species share a very similar androecium of dimorphic stamens, which is correctly described for the first time. *Plukenetia stipellata* differs from the closely related South American and West Indian species, *P. volubilis*, by its stipellate leaf blade base, shorter styles and longer slender stamens. Two new combinations, **P. serrata** and **P. lehmanniana**, are proposed. A key to the 11 species in the Neotropics is provided.

*Plukenetia* L. is a pantropical genus of 16 species of twining vines and lianas belonging to the Euphorbiaceae. The genus is notable for its four-carpellate ovary, styles that are partially to entirely fused and often massive, and scandent habit. Other diagnostic characters include one or more pairs of adaxial basilaminar glands, numerous stamens, and pistillate flowers with four sepals. Two new species of *Plukenetia* were identified while working on preliminary revisional studies of the genus and the treatment of the tribe Plukenetieae for the *Flora of the Guianas*. Since many of the neotropical species are poorly known and specimens are frequently misidentified, it seems appropriate to provide a synopsis of the 11 neotropical species. This will also serve to introduce several nomenclatural and taxonomic changes, and will make available the new names and combinations for floristic studies prior to a complete revision of the genus. While species of *Plukenetia* are for the most part well defined, some collections appear to be morphologically intermediate or to combine characters of several species and cannot be easily placed. Field studies and more collections are needed to determine the status of these anomalous collections before a monograph can be completed.

*Plukenetia* belongs to the tribe Plukenetieae of the uniovulate subfamily Acalyphoideae (sensu Webster 1975). Members of Acalyphoideae characteristically lack latex, and have eglandular inflorescence bracts, apetalous flowers and staminate flowers with valvate sepals. The tribe Plukenetieae is distinguished by the character combination of entire styles that are partly to completely connate and often massive, and bisexual racemose or spicate (or rarely paniculate) inflorescences bearing cymose clusters of flowers with pistillate flower(s) at the basalmost node(s) (unisexual inflorescences are found in a few taxa including *Acidoton* Sw. and a small percentage of species of *Tragia* L.). Members are frequently scandent, a very unusual habit in the family. Webster (1975) divided the tribe into two subtribes, the Tragiinae characterized by the presence of stinging hairs and the Plukenetiinae, which lack stinging hairs. The tribe was monographed by Pax (1890) and Pax and Hoffmann (1919, 1931; their subtribe Plukenetiinae is equivalent to Webster's tribe Plukenetieae), and more recently, pollen morphology was surveyed (Gillespie, in press).

The circumscription of genera belonging to subtribe Plukenetiinae (sensu Webster) has changed considerably over the last 150 years [although the subtribe was not formally recognized prior to Webster (1975), changes in its constituent genera can be traced]. The three genera, *Angostyles* Benth., *Astrococcus* Benth., and *Haematostemon* (Muell. Arg.) Pax & K. Hoffm., distinguished by their shrub or tree habit and tricarpellate ovary, are well defined and have been consistently recognized by most authors; they appear to be more closely related to each other than to *Plukenetia* (Gillespie, in press). The remaining genera may be recognized by their

twining vine or liana habit and, with one exception, by a four-carpellate ovary. Baillon (1858), Bentham (1880), Mueller (1866), and Pax (1890) adopted a broad generic concept for species with a scandent habit. Mueller and Baillon recognized only two genera, *Plukenetia* (called *Sajorum* by Baillon) and *Fragariopsis* A. St. Hil. (=*Vigia* Vell. Conc.), while Bentham and Pax recognized only *Plukenetia*; all these authors subdivided *Plukenetia* into three to six sections. In contrast, Pax and Hoffmann (1919, 1931) recognized seven genera. In addition to *Plukenetia* and *Fragariopsis*, they treated *Anabaena* Adr. Juss. (which they renamed *Anabaenella*, but is now correctly known as *Romanoa* Trev. St. Léon; see Gillespie, in press; Radcliffe-Smith 1980), *Angostylidium* (Muell. Arg.) Pax & K. Hoffm. (=*Tetracarpidium* Pax), and *Pterococcus* Hassk. as genera rather than sections of *Plukenetia*, created a new genus, *Apodandra*, for two species of *Plukenetia*, and described a new monotypic genus, *Eleutherostigma*. More recently, Webster (1975) recognized four genera among species having the vine or liana habit, *Plukenetia*, *Eleutherostigma*, *Fragariopsis* (=*Vigia*) and *Anabaena* (=*Romanoa*).

In the present treatment only two genera, *Plukenetia* and *Romanoa*, are recognized among scandent members of subtribe Plukenetiinae; both *Eleutherostigma* and *Vigia* are included within *Plukenetia*. The principal defining synapomorphies of *Plukenetia* are the four-carpellate ovary and the associated character of four pistillate sepals. *Romanoa* is considered a distinct monotypic genus on the basis of its pistillate flowers with a tricarpellate ovary and five sepals, and the sister taxon of *Plukenetia* on the basis of numerous shared characters of floral and pollen morphology (Gillespie, in press). An alternative and phylogenetically equivalent treatment would be to consider *R. tamnoides* (Adr. Juss.) R.-Smith as the most plesiomorphic species of *Plukenetia*. *Plukenetia* as circumscribed here includes 11 neotropical species, one species from southeast Asia, three from Africa, and one from Madagascar.

The neotropical monotypic genera, *Eleutherostigma* and *Vigia*, are included within *Plukenetia* since neither are defined by unique characters considered significant at the generic level. The defining character of *Eleutherostigma*, shortly connate rather than mostly to entirely connate styles, appears to be only a quantitative difference in degree of style fusion and represents only one end of a continuum (Fig. 1). Likewise, the single unique feature characterizing *Vigia*, an unusually enlarged globose staminate receptacle, is simply a difference in size, since all species have globose or convex receptacles [refer to the discussions under *P. lehmanniana* (Pax & K. Hoffm.) Huft & L. J. Gillespie and *P. serrata* (Vellozo) L. J. Gillespie in the section "Enumeration of Taxa" below for a more complete discussion]. When *Eleutherostigma* and *Vigia* are excluded, *Plukenetia* is a paraphyletic genus lacking any uniquely derived defining characters.

Pax and Hoffmann (1919, 1931) recognized two sections in their narrowly defined, neotropical genus *Plukenetia*, sects. *Euplukenetia* (=sect. *Plukenetia*) and *Cylindrophora* [also considered sections by Mueller (1866) in his more broadly defined circumscription of the genus]. In this treatment of neotropical species, two informal species groups are outlined, which correspond to more broadly circumscribed versions of the two sections. However, recognition of a formal sectional classification will await revision of the paleotropical species and a phylogenetic study of the genus.

Neotropical species of *Plukenetia* may be divided into two informal species groups based on style shape, androecium morphology, pollen exine structure, fruit size, and leaf architecture. The first group (species group 1, "Cylindrophora") is characterized by styles that are only partly fused into a cylindrical stylar column (mostly fused in *P. volubilis* L. and mostly free in *P. lehmanniana*; Figs. 1A–C, 9C), androecia in which all stamens have distinct filaments (Fig. 9D–E), pollen with a foveolate tectum (Figs. 4–6; Gillespie, in press), large fruit, and palmately veined or triplinerved, cordiform, ovate or broadly elliptic leaves (Figs. 3, 9A). The following four species comprise this group: *P. lehmanniana*, *P. polyadenia* Muell. Arg., *P. stipellata* L. J. Gillespie, and *P. volubilis*.

The second species group (species group 2, "Euplukenetia") is characterized by entirely fused styles (Figs. 1D, 10H), all or at least most anthers sessile (Fig. 10G), pollen with a reticulate tectum (Figs. 7–8; Gillespie, in press), small dry capsules (except *P. serrata*), and elliptic, pinnately veined leaves (Figs. 2, 10A; except *P. verrucosa* Smith). Three species belonging to this group, *P. brachybotrya* Muell. Arg., *P. loretensis*

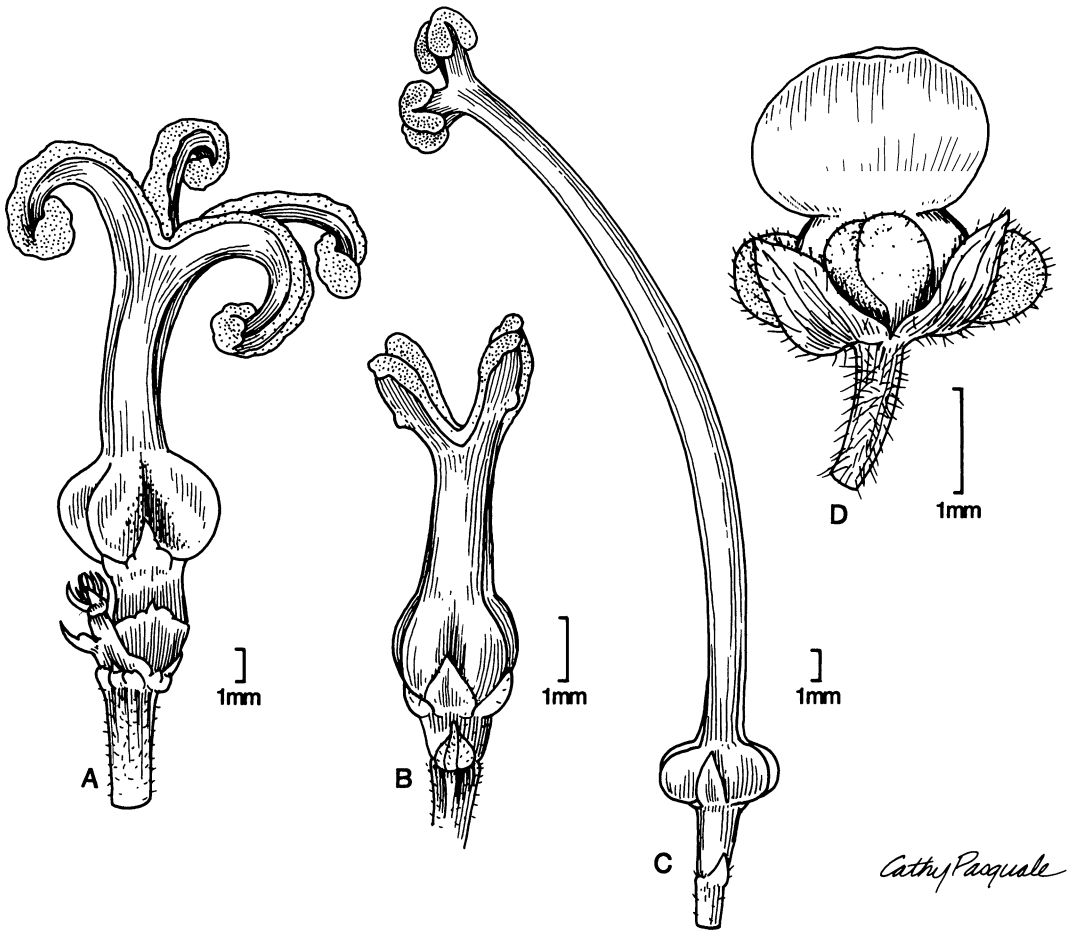
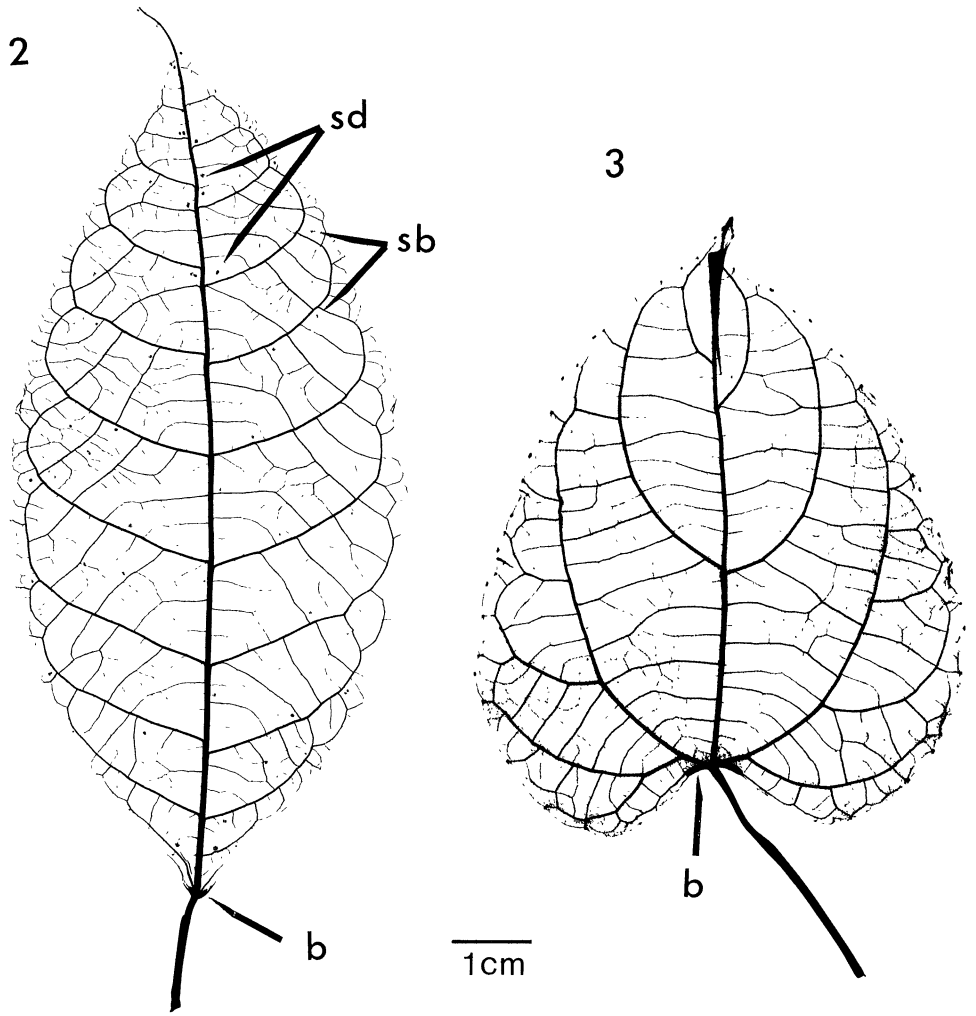



FIG. 1. Pistillate flowers of *Plukenetia* showing variation in style morphology. A. *P. lehmanniana* (*Acevedo & Daly 1691*, US). B. *P. polyadenia* (*Black 52-14173*, P). C. *P. volubilis* (*Zarucchi 2378*, US). D. *P. verrucosa* (*Irwin 48796*, US); note the pubescent and indistinctly bilobed ovary lobes between the sepals. Note the cyme axis and bracteole(s) subtending the pedicel in A–C (not shown in D).

Ule and *P. serrata*, have androecia in which all anthers are sessile on a globose receptacle. *P. multiglandulosa* Jabl., *P. penninervia* Muell. Arg., and *P. supraglandulosa* L. J. Gillespie form a closely related species complex (referred to here as the *P. penninervia* species complex) characterized by androecia consisting of two distinct types of stamens and by a short stout-cylindrical stylar column (Fig. 10H). This unusual type of androecium, correctly described here for the first time, consists of an outer whorl of four (or rarely five) stamens having filaments and an inner cluster of sessile anthers densely crowded on a small globose receptacle (Fig. 10G). Previous authors have overlooked the dimorphic nature of the stamens and have usually described the stamens simply as having very short filaments. *Plukenetia verrucosa* also has dimorphic stamens but differs in having a subglobose stylar column and narrowly cordiform or ovate triplinerved leaves.

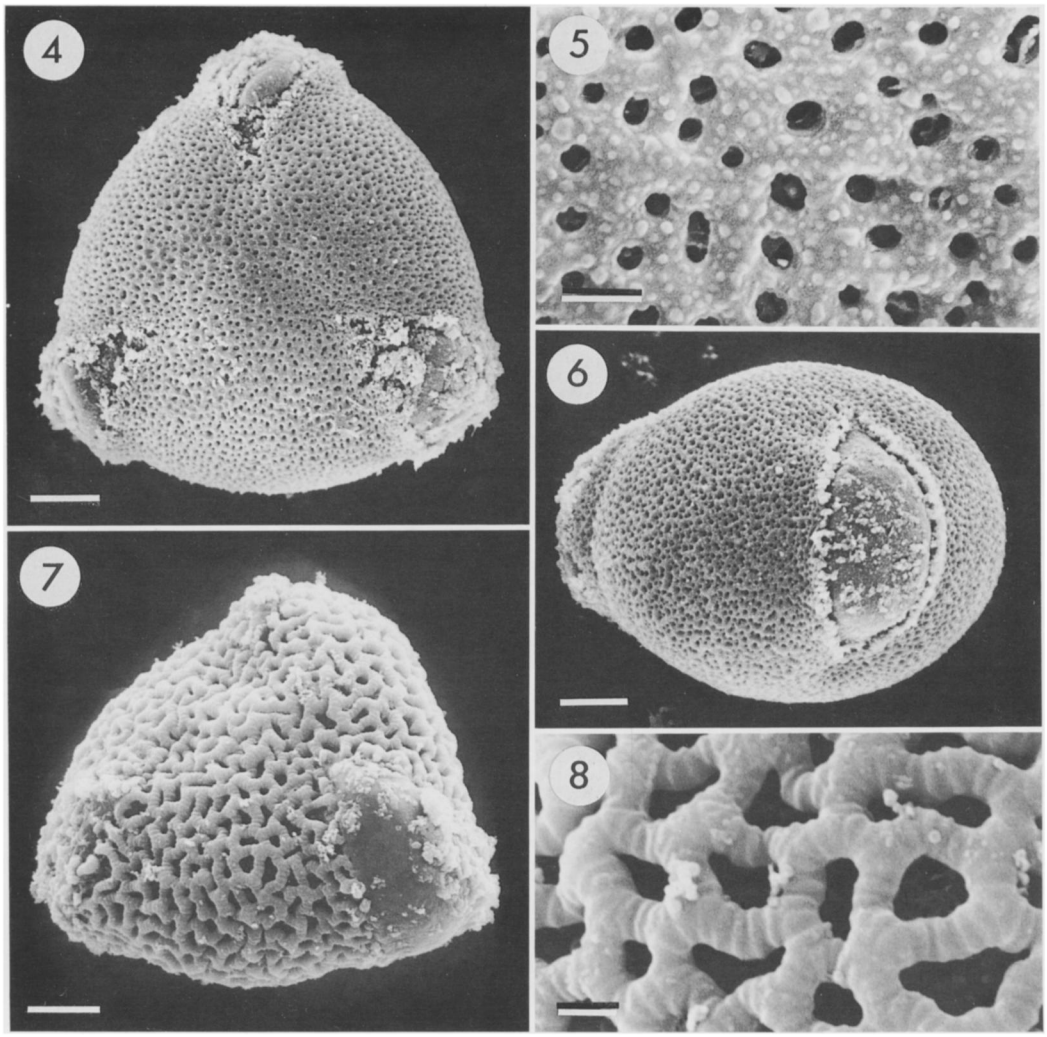
Using the hypothesis of *Romanoa* as the sister taxon of Plukenetia, many of the above characters can be tentatively polarized. *Romanoa* is characterized by palmate-veined cordiform leaves, partly fused styles, stamens with distinct filaments, and a fossulate-foveolate pollen tectum. This would indicate that entirely fused styles, sessile anthers, and reticulate pollen tectum are synapomorphies of the second species




FIGS. 2–3. Leaf Architecture of *Plukenetia*. b = basilaminar gland pair; sd = scattered laminar glands on adaxial surface; sb = scattered laminar glands on abaxial surface. 2. *P. supraglandulosa* (*Granville 3626*, CAY). 3. *P. stipellata* (Gillespie 413, US).

group, and that pinnately veined leaves are a synapomorphy within that group.

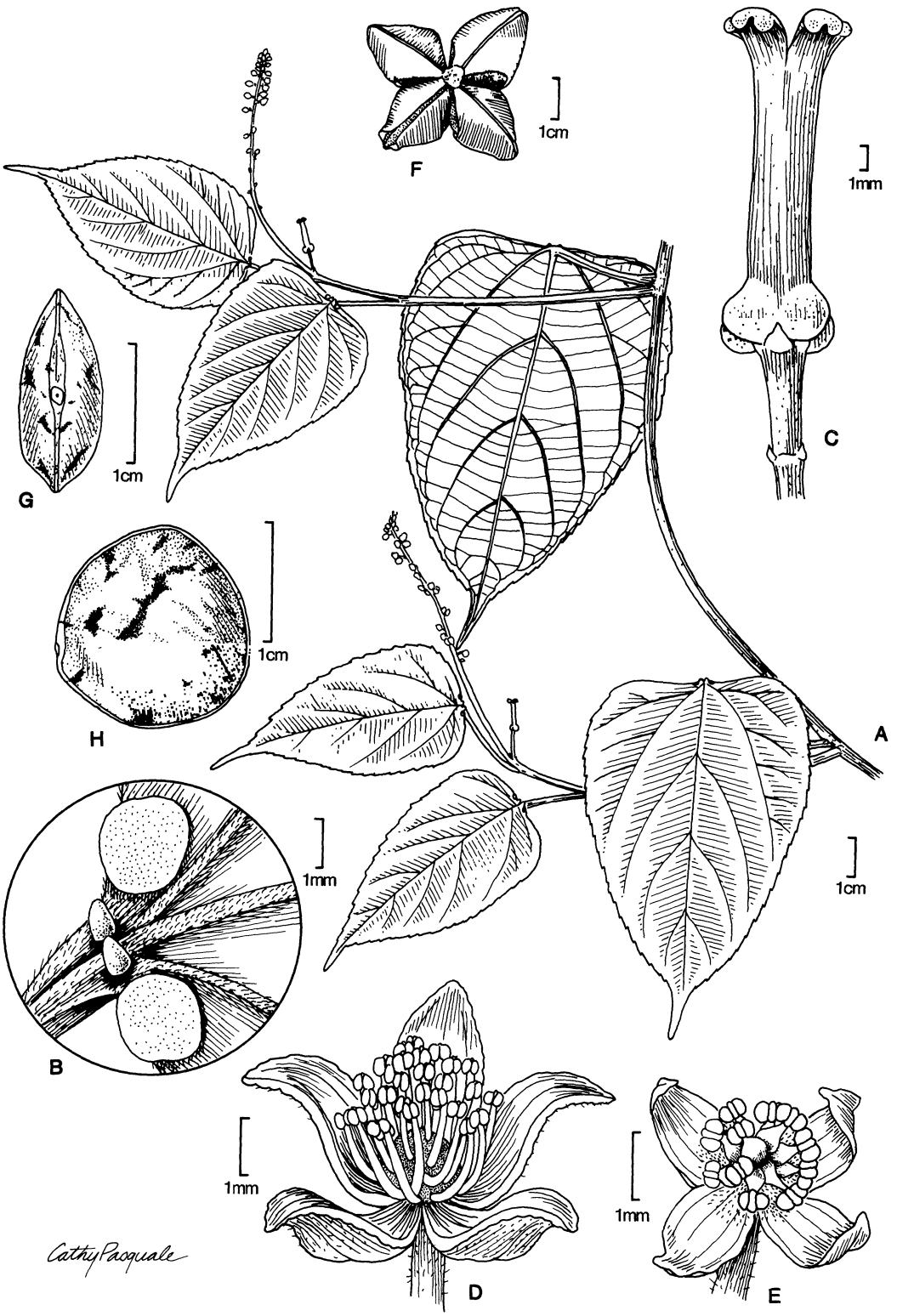
The presence of stipels or a glandular knob at the petiole apex is a feature unique to *Plukenetia* among members of the tribe Plukenetieae. The following three species have paired stipels: *P. serrata*, *P. stipellata*, and *P. verrucosa*; while the following have a single glandular knob: *P. lehmanniana*, *P. polyadenia*, and *P. volubilis*. Since a small knob is occasionally present between the pair of stipels in *P. stipellata*, these two structures appear to be distinct and probably not directly homologous. The stipels are most likely comparable to the similarly placed stipels of *Dalechampia* L., a genus related to the Plukenetieae (in which it is sometimes included as a separate subtribe; Webster, in press), and may have originated from paired acropetiolar glands that are commonly found in species of Euphorbiaceae. They are presumably not homologous with morphologically similar structures in other families. "Stipels" is used here in a broad sense to indicate a paired appendage located at the leaf blade base and not in the strict functional sense of secondary stipules at the base of leaflets of a compound leaf.




FIGS. 4–8. Pollen morphology of *Plukenetia*. 4–6. *P. stipellata* (*Gillespie 413*, US). 7–8. *P. supraglandulosa* (*Cowan 38204*, US). 4, 7. Polar view. Scale bars = 10 μm. 5. Equatorial view. Scale bar = 10 μm. 6, 8. Exine sculpture. Scale bars = 2 μm.

While the majority of species are relatively well defined, a number of collections appear to be intermediate, to combine characters of several species, or to be somewhat distinct. These anomalous collections are noted and briefly described. Although at least some may represent new species, our knowledge of them is inadequate and additional collections are needed to determine their status. Further collections are also necessary to determine more precisely the range of variation in known species and the existence of possible hybrids. It is hoped that by drawing attention to these problematic collections, field botanists will be encouraged to collect populations of *Plukenetia* more extensively, particularly in poorly known and undercollected areas of Amazonian Brazil and the eastern slopes of the Andes.

One explanation for the above problematic collections is the existence of species complexes consisting of populations that are geographically or altitudinally isolated but morphologically little differentiated. An example is the *P. penninervia* species complex consisting of one



species widespread in Mesoamerica and Venezuela and a number of isolated populations scattered throughout South America (*P. multiglandulosa, P. supraglandulosa* and the anomalous Colombian population of *P. penninervia*). *Plukenetia volubilis* and *P. stipellata* comprise a second species complex. While considered as distinct but closely related species here, they could alternatively be treated as subspecies of a single variable widespread species. *Plukenetia brachybotrya* and the numerous problematic collections cited under that species may represent a third species complex.

## Key to the Neotropical Species of *Plukenetia*

1. Leaf blade pinnately veined, acute, obtuse, or rounded at base; glandular knob lacking at midrib base, stipels present only in *P. serrata*; scattered laminar glands usually present on lower leaf surface (except in *P. penninervia* and *P. serrata*); styles entirely connate, 1–4 mm long; all anthers sessile or stamens dimorphic with inner anthers sessile and outer with short filaments (as in Fig. 10G).
   2. Fruit ca. 4 cm or more in diam., fleshy; pistillate flowers 1–10 per inflorescence; all anthers sessile and scattered on globose receptacle, receptacle 2 mm or more in diam., clearly visible between anthers; stylar column massive-obovoid; pair of stipels present adaxially at midrib base ..... 7. *P. serrata*
   2. Fruit 1–2 cm in diam., capsular; pistillate flower 1 per inflorescence; all or only some anthers sessile and densely crowded on globose receptacle, receptacle less than 1 mm in diam., not visible between anthers; stylar column various; stipels absent.
      3. Stamens of one type: 15–50 sessile anthers on globose receptacle; stylar column massive-globose or slender-cylindrical, (1) 2–4 mm long.
         4. Stylar column slender-cylindrical; ovary and capsule with pointed horn on each carpel; stamens 15–25; basilaminar glands in 1 to several pairs ..... 3. *P. loretensis*
         4. Stylar column massive-globose; ovary and capsule with rounded tubercle on each carpel; stamens (24) 30–50; basilaminar glands in a single pair ..... 1. *P. brachybotrya*
      3. Stamens of two types: outer whorl of 4 (5) stamens with filaments, inner cluster of 6–12 sessile anthers on globose receptacle; stylar column stout-cylindrical, 1–2 (3) mm long.
         5. Basilaminar glands in 3–5 pairs; young shoots and petioles densely hirsute; blade hirsute below, hairs persistent ..... 4. *P. multiglandulosa*
         5. Basilaminar glands in 1–2 (3) pairs; young shoots and petioles puberulent; blade sparsely puberulent below, often becoming glabrous.
            6. Scattered laminar glands absent or rarely 1–8 near margin on lower leaf surface only; leaf blade chartaceous to coriaceous, mostly subcoriaceous, margin distinctly serrulate and often distinctly glandular; inflorescence 1–3 cm long (to 6 cm only in Colombia) ..... 5. *P. penninervia*
            6. Scattered laminar glands numerous, present on both upper and lower leaf surfaces; leaf blade chartaceous, margin minutely serrulate, appearing undulate, never distinctly glandular; inflorescence 2–8 cm long ..... 9. *P. supraglandulosa*

1. Leaf blade palmately veined or triplinerved, cordate, rounded, or broadly obtuse at base; glandular knob or stipels present adaxially at midrib base; scattered laminar glands absent on lower leaf surface; styles partly to entirely connate, 1.5–30 mm long; all stamens with distinct filaments or stamens dimorphic with inner anthers sessile (only in *P. verrucosa*).
   7. Stylar column globose, 1.5–2 mm long, styles entirely connate; outer stamens with filaments, inner anthers sessile; fruit less than 1.5 cm in diam., 4-lobed, capsular ..... 10. *P. verrucosa*
   7. Stylar column cylindrical, 2–30 mm long, styles only partly connate (sometimes free only at tip); all stamens with filaments; fruit greater than 2.5 cm in diameter, 4-lobed or subglobose, fleshy or capsular.

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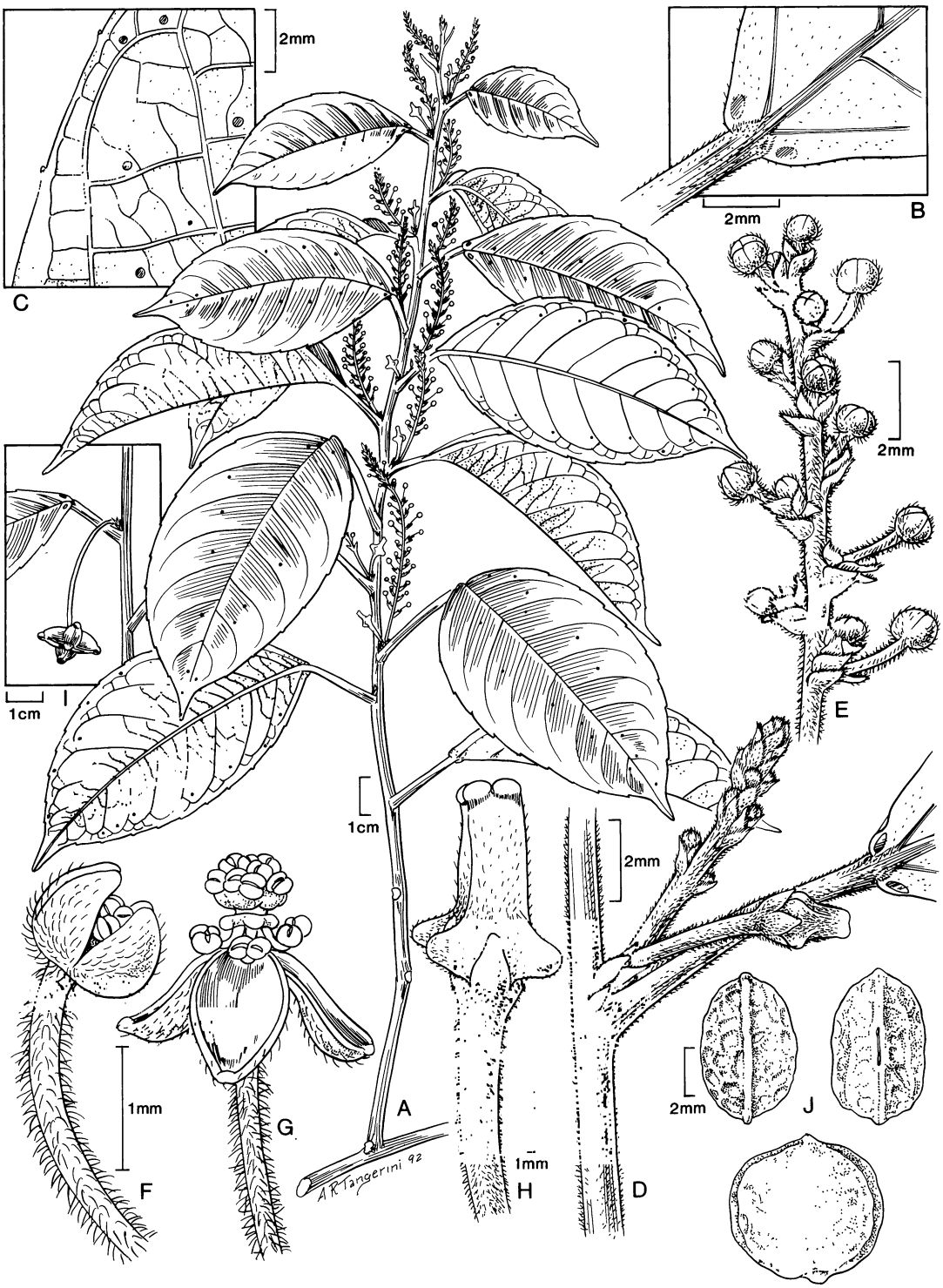
FIG. 9. *Plukenetia stipellata*, with staminate flower of *P. volubilis* for comparison. A. Habit (*Leisner 2068*, US). B. Adaxial leaf base showing pair of stipels between pair of basilaminar glands (*Gillespie 413*, from FAA preserved material). C. Pistillate flower (*Gillespie 413*, US). D. Staminate flower (*Gillespie 413*, US). E. Staminate flower of *P. volubilis* (*Vargas 13994*, US). F. Capsule (*Pittier 324*, US, dried specimen). G. Seed, ventral view (*Smith 1651*, US). H. Seed, lateral view (*Smith 1651*, US).



8. Styles free for one half or more of length, column 3–6 mm long, arms 3–6 mm long; staminate sepals 5; ligulate (strap-shaped) disc segments present between stamens; fruit subglobose, squarish in cross-section ..... 2. *P. lehmanniana*
8. Styles free for less than one half of length, column 2–30 mm long, arms 1–2.5 (3) mm long; staminate sepals 4 or 5; staminate disc segments absent, or if present minute and not ligulate; fruit various.
   9. Stylar column 3–7 mm long; fruit subglobose, squarish in cross-section, greater than 6 cm in diam., indehiscent; staminate bud narrowly oblong-ellipsoid; filaments 2–2.5 mm long; inflorescences mostly unisexual, dimorphic, pistillate inflorescence with 3–4 (10) flowers; leaf base rounded or broadly obtuse ..... 6. *P. polyadenia*
   9. Stylar column 6–30 mm long; fruit 4-lobed, 2.5–4 (6) cm in diam., dehiscent; staminate bud subglobose; filaments 0.4–1.2 mm long; inflorescence bisexual with one or two pistillate flowers at basal nodes; leaf base cordate or truncate.
      10. Pair of stipels present adaxially at petiole apex, glandular knob minute or lacking between stipels; stamens 25–40, filaments slender, 1–1.2 mm long; stylar column 6–11 mm long; staminate sepals 5, rarely 4 ..... 8. *P. stipellata*
      10. Pair of stipels absent, single glandular knob present adaxially at petiole apex; stamens 16–30, filaments stout-conical, 0.4–0.5 mm long; stylar column 15–30 mm long; staminate sepals 4 ..... 11. *P. volubilis*

## Enumeration of Taxa

1. Plukenetia brachybotrya Muell. Arg., Linnaea 34: 158. 1865. *Apodandra brachybotrya* (Muell. Arg.) J. F. MacBr., Field Mus. Nat. Hist., Bot. Ser. 13(3a): 117. 1951.—Type: Peru, *Herb. Pavon* (holotype: G-BOIS!; isotypes: G!, G-DC!)

*Plukenetia buchtienii* Pax, Feddes Repert. 7: 110. 1909. *Apodandra buchtienii* (Pax) Pax & K. Hoffm., Pflanzenr. IV.147.IX.(Heft 68): 21. 1919.—Type: Bolivia, Charopampa near Mapiri, *Buchtien 1962* (holotype: presumably B, destroyed; lectotype, here designated: US!; isolectotype: NY!).

*Distribution and habitat.* Found in the western part of the Amazon Basin in Brazil (Acre and possibly Amazonas, Mato Grosso, and Pará, see discussion below), Ecuador, Peru, and Bolivia. A twining vine or liana found in wet lowland and lower montane forest, often in disturbed areas, sea level to 900 m.

*Representative specimens examined.* Bolivia. **Beni:** Serrania del Pilon Lajas, prov. Ballivian, *Smith 13222* (MO). **La Paz:** 27.8 km N of Caranavi, 15°33'S, 67°45'W, *Croat 51620* (F, MO); Tuiri, on left bank of Río Mapiri, *Krukoff 10753* (G, F, K, MO, NY, US). **Pando:** cerca de Porvenir en dirección a Chivé, *Casas & Casas 8149* (NY).

Brazil. **Acre:** 35 km from Rio Branco on Rio Branco-Santa Rosa road, *Lowrie et al. 315* (GH, MO, NY, US).

Ecuador. **Napo:** Estacion Biologica Jatun Sacha, 8 km E of Misahualli, 1°4'S, 77°36'W, *Cerón & Iguago 5474* (DAV, MO).

Peru. **Huánuco:** Bosque Nacional de Iparia, road to Ayamira along Río Pachitea, *Schunke 1314* (NY, US). **Loreto:** 12.5 km SW of Iquitos, *Croat 20058* (GH, MO, NY, P, US). **Madre do Dios:** Manú Park, Cocha Cashu uplands, 11°45'S, 71°0'W, *Núñez 6087* (F, MO, NY).

The species may be distinguished from the closely related and vegetatively similar species, *P. loretensis*, by its globose stylar column (typically 2–3 mm in diam.), capsule with rounded tubercle on each carpel lobe, and anthers that are typically 30–50 in number.

*Plukenetia buchtienii* is treated here as a synonym of *P. brachybotrya*. *Plukenetia brachybotrya*

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Fig. 10. *Plukenetia supraglandulosa*. A. Habit. B. Adaxial leaf base showing pair of basilaminar glands. C. Abaxial leaf surface showing scattered laminar glands. D. Leaf axil with young inflorescence showing basal position of pistillate flower. E. Terminal section of inflorescence showing staminate flower buds in condensed cymes. F. Staminate flower bud beginning to open. G. Staminate flower. H. Pistillate flower. I. Immature capsule. J. Seed, showing dorsal, ventral, and lateral views, respectively. (A–C, F, G, I based on *Granville 3626*, CAY, US; D, E, H based on *Cowan 38204*, US; J based on *Granville et al. 10783*, CAY).

has been considered a very poorly known species with descriptions based primarily on Mueller's (1866) partly incorrect description in *Flora Brasiliensis*. Although Mueller originally described the species as having about 30 anthers, as distinct from *P. penninervia* with 12–15 anthers, the following year Mueller (1866) reversed the numbers and described *P. brachybotrya* as having 12–15, and the latter with 20–30 anthers. This mistake persisted until the present with anther number always given incorrectly as 12–15 for *P. brachybotrya* (e.g., MacBride 1951; Pax and Hoffmann 1919). The only other characters given by MacBride to distinguish the species from *P. buchtienii* were differences in leaf shape and number of secondary veins, neither of which are valid when the full range of variation is examined.

Both *P. buchtienii* and *P. loretensis* (Pax and Hoffmann 1919), and, subsequently, *P. brachybotrya* (MacBride 1951) were segregated as a distinct genus, *Apodandra*, based on the androecium of sessile anthers on a globose receptacle. However, both of these character states are shared with other species of *Plukenetia*. *Plukenetia serrata* also has all anthers sessile on a globose receptacle, while the remaining members of species group 2 (*P. penninervia* species complex and *P. verrucosa*) have most anthers sessile on a globose receptacle.

Several collections, particularly the few known from central and eastern Amazonian Brazil, appear to diverge from those of typical *P. brachybotrya*; these aberrant collections are included here, but additional collections may show that they represent distinct species. The single collection (*Lowrie et al. 30*) seen from the Brazilian state of Amazonas has an androecium of ca. 20 anthers, a depressed globose stylar column distinctly wider than long (ca. 1 × 1.8 mm), and a narrower subcoriaceous leaf blade. Collections from Pará and Mato Grosso, Brazil (*Plowman et al. 8741, Sperlin et al. 5837,* and *Thomas et al. 4732*) have distinctly larger obovate stylar columns (3.5–4.5 mm long). Several collections from Peru (e.g., *Croat 20058* and *Davidson 5310*) have smaller stylar columns (1–2 mm long) and longer inflorescences and in some cases fewer anthers (ca. 25). A number of otherwise typical collections from Madre de Dios, Peru appear to have fleshy fruit ca. 2.5 cm in diameter, much larger than the normal dry capsules. Large fleshy fruit and typical capsules are both present on specimens of one collection (*Gentry 43598*), suggesting that the fleshy fruits are abnormal.

2. **Plukenetia lehmanniana** (Pax & K. Hoffm.) Huft & L. J. Gillespie, comb. nov.—*Eleutherostigma lehmannianum* Pax & K. Hoffm., Pflanzenr. IV.147.IX.(Heft 68): 11. 1919.—TYPE: Colombia, Nariño, Ricaurte, 1000–1400 m, *Lehmann 5158* (holotype: B, destroyed; lectotype, here designated: K!; isolectotype: K!). Fig. 1A.

*Plukenetia chapoensis* Croizat, Caldesia 2: 431. 1944.—TYPE: Colombia, Boyaca, region of Mt. Chapón, 3600 ft, *Lawrance 276* (holotype: A!; isotypes: BM! K! MO! NY! US!).

*Distribution and habitat.* Known only from Colombia and Ecuador, where it appears to be restricted to the area west of the Andean divide in Ecuador and to the Pacific coast region and mountain valleys of southern and central Colombia. A robust, somewhat woody, twining vine found in seasonal to wet, lowland to montane forest, 150–2100 m.

*Representative specimens examined.* COLOMBIA. **Caldas:** Pacora, *Daniel 4943* (US). **El Valle:** hoya del Río Cali, vertiente izquierda del Río Pichindé, El Cairo, *Cuatrecasas 21971* (US).

ECUADOR. **Carchi:** vicinity of Chical, W of Maldonado on trail to Penas Blancas, *Gentry & Shupp 26396* (DAV, MO). **Esmeraldas:** road from Lita to San Lorenzo, 19 km N of Lita, *Acevedo & Daly 1658* (NY), *1691* (US). **Guayas:** Teresita, 3 km W of Bucay, *Hitchcock 20490* (NY, US). **Los Ríos:** Río Palenque Biological Station, km 56 Quevedo-Santo Domingo, *Dodson 5771* (MO, US); Río Palenque Field Station, halfway between Quevedo and Santo Domingo de los Colorados, *Gentry 9701* (DAV, MO). **Pichincha:** Reserva Forestal ENDESA, Quito-Puerto Quito road, 10 km N of main road, km 113, 00°05'N, 79°02'W, *Acevedo et al. 1658* (US), *1694* (US); 20 km W of Santo Domingo de los Colorados, *Cazalet & Pennington 5089* (DAV, K, NY, US).

Pax and Hoffmann distinguished their monotypic genus *Eleutherostigma* from *Plukenetia* and related genera based on the styles being shortly connate rather than entirely or mostly connate. Styles are connate for one-third to one-half of their length into a cylindrical column with the four style arms slender-cylindrical and recurved when mature (Fig. 1A). Among species with styles partly fused into a cylindrical stylar column (species group 1), *P. polyadenia* has styles

connate for approximately two-thirds of their length (Fig. 1B), while *P. stipellata* (Fig. 9C) and *P. volubilis* (Fig. 1C) have styles connate for seven-eighths or more. The character of style morphology used to define *Eleutherostigma* is merely a quantitative difference in degree of style fusion. Since there are no significant floral, vegetative or palynological qualitative characters distinguishing the genus from *Plukenetia*, *Eleutherostigma* is not worthy of generic recognition [Huft (unpubl. manuscript) previously came to this conclusion]. Indeed, *P. lehmanniana* fits easily within the boundary of species group 1 and appears to be closely related to the other three members. Croizat (1944) previously recognized this alliance by placing his new species *P. chapoensis* (=*P. lehmanniana*) in sect. *Cylindrophora*.

The species may be distinguished by the character combination of mostly free styles, ligulate staminate disc segments, large fleshy subglobose fruit, and single conspicuous knob at the petiole apex. *Plukenetia lehmanniana* is the only species of *Plukenetia* found west of the Andes in Ecuador and southwest Colombia; records of *P. volubilis* in this area (Dodson and Gentry, 1978; Dodson et al., 1985) appear to be based on misidentified specimens of *P. lehmanniana*.

3. PLUKENETIA LORETENSIS Ule, Verh. Bot. Vereins. Prov. Brandenburg 81. 1980.—*Apodandra loretensis* (Ule) Pax & K. Hoffm., Pflanzenr. IV.147.IX.(Heft 68): 21. 1919.—TYPE: Peru, Loreto, Iquitos, Apr 1903, *Ule 6837* (isotype: G!, photo F 24572!).

*Distribution and habitat.* Found in the upper and middle Amazon Basin in Peru, Bolivia, and Brazil (Amazonas, Mato Grosso, and Rondônia), and in southern Venezuela and southeast Guyana. A twining vine or slender liana in moist to wet, lowland forest, sea level to 700 m.

*Representative specimens examined.* BOLIVIA **Beni:** 3 km E of Piberalta on road to Guagaramerín, 11°00'S, 66°5'W, *Solomon 7972* (MO, NY)

BRAZIL. **Amazonas:** Rod. Transamazonica a 400 km de Humaita, 7°15'S, 60°00'W, *Cid 5983, INPA 127.449* (F, NY); Mun. São Paulo de Olivença, Belem Creek, *Krukoff 8791* (A, G, K, MO, NY, P, US). **Mato Grosso:** BR-174, Aripuanã, *Silva & Rosário 4795* (MO, NY). **Rondônia:** BR-364, Porto Velho-Cuiaba, 12°13'S, 60°61'W, *Cid et al. 4359, INPA 120.732* (MO, NY).

GUYANA. Kanasenay, *Guppy 203, FD 7179* (NY).

PERU. **Loreto:** Río Nanay, Purto Almendrez, *Gentry et al. 15598* (DAV, F, MO); Río Putumayo, at mouth of Río Zubineta, *Klug 2178* (A, GH, K, MO, NY, US). **San Martín:** SW of Aeropuerto de Tocache Nuevo, *Schunke 3686* (GH, G, MO, NY, US).

VENEZUELA. **Amazonas:** La Neblina Base Camp, 0°50'N, 66°10'W, *Leisner & Funk 16526* (DAV, MO); Cerro Sipapo, Base Camp, *Maquire & Politi 27371* (NY, US). **Bolívar:** Ikabaru, near Campo Diamentifero de Uaiparé, *Bernardi 6649* (NY).

*Plukenetia loretensis* is unique among neotropical species in having styles entirely fused into a slender elongate-cylindrical stylar column, and a distinctly four-horned ovary and mature capsule. These characters, along with an anther number of 15–25 and basilaminar glands frequently in multiple pairs on either side of the midrib, distinguish it from the vegetatively similar species, *P. brachybotrya*.

4. PLUKENETIA MULTIGLANDULOSA Jabl., Mem. New York Bot. Gard. 17: 143. fig. 23. 1967.—TYPE: Venezuela, Amazonas, Cerro Parú, 1800 m, *Cowan & Wurdack 31400* (holotype: NY!; isotypes: NY!, US!).

*Distribution and habitat.* Known only from a single collection on Cerro Parú where it is found in montane forest on talus at base of escarpment at 1800 m.

The species may be distinguished from the closely related species, *P. penninervia* and *P. supraglandulosa*, by its persistent yellow-hirsute indumentum and multiglandular leaf base composed of three to five pairs of basilaminar glands. The androecium, previously described inaccurately, consists of an outer whorl of four stamens with short filaments and an inner cluster of eight to ten sessile anthers on a globose receptacle, very similar to the androecium of *P. supraglandulosa* (Fig. 10G).

5. PLUKENETIA PENNINERVIA Muell. Arg., Linnaea 34: 158. 1865.—TYPE: Venezuela, near Biscaina, *Fendler 2412* (holotype: G-DC!, photo F 7110!; isotypes: K!, GH!, MO!).

*Plukenetia angustifolia* Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 314. 1864.—TYPE: Honduras, Atlantida Dept., Lancetilla Valley, near Tela, *Standley 56708* (holotype: F!; isotypes: A!, K!, US!).

*Distribution and habitat.* Widespread from southern Mexico to Venezuela. A twining vine

in disturbed areas of dry to wet, lowland to montane forest, sea level to 1500 m.

*Representative specimens examined.* BELIZE. Big Creek, *Schipp 156* (BM, G, K, NY, UC, US).

COSTA RICA. **Puntarenas:** Rincón de Osa, *Utley & Utley 1215* (F).

GUATEMALA. **Izabal:** vicinity of Quiriguá, *Steyermark 23921* (GH, US). **Peten:** Dos Lagunos, 5 km on Ixcanrio Road, *Elias 8361* (MO, US).

MEXICO. **Oaxaca:** Chiltepec and vicinity, *Martínez-Calderón 291* (A, UC, US). **Tabasco:** La Palma, Balancan, *Matuda 3288* (A, K, NY). **Yucatan:** Tuxpeña, Campeche, *Lundell 1368* (US).

NICARAGUA. **Río San Juan:** 3.5 km NE of Boca de Sabalo, 11°3′N, 84°26′W, *Moreno 25463* (DAV, F, MO). **Zelaya:** road between Waní and Siuna near Río Matís, 13°43′N, 84°49′W, *Pipoly 4693* (DAV, MO).

PANAMA. **Colon:** Santa Rita Ridge, 9°20′N, 79°45′W, *McPherson 8461* (MO).

VENEZUELA. **Bolívar:** Río Toro, between Río La Reforma and Puerto Rico, N of El Palmar, *Steyermark 88148* (F, GH, K, NY, P, U, US). **Delta Amacuro:** ca. 13 km by road ESE of town of Sierra Imata, 8°23′N, 62°23′W, *Davidse & González 16501* (DAV, MO, NY). **Distrito Federal:** along Río Chichiriviche, 1–2 km S of Chichiriviche, 10°32′30″N, 67°14′30″W, *Steyermark & Espinosa 112709* (F, MO, NY). **Falcón:** Sierra de San Luis, Montana de Paraguariba, 3 km E of Cerro Galicia, *Flora Falcón 617* (DAV, MO). **Miranda:** Los Caracas-Cabo Codera, *Aristeguieta 4852* (NY, US). **Portuguesa:** between La Estacion and La Laguna, 15–18 km NNW of Ospino, 9°25–27′N, 69°30–31′W, *Steyermark et al. 127019* (F, MO, U). **Zulia:** entre las Tres Marías (10°25′N, 70°55′W) y Río Chiquito, *Bunting & Stoddart 8913* (DAV, NY).

*Plukenetia penninervia* is the most common and widespread species in the *P. penninervia* species complex, which is characterized by dimorphic stamens and a short stout-cylindrical stylar column. The species may be distinguished from *P. multiglandulosa* by its glabrescent leaves and single pair of usually circular basilaminar glands (rarely several pairs in collections north of Honduras only), and from *P. supraglandulosa* by the absence of scattered laminar glands (occasionally present on the lower leaf surface but never on the upper surface apart from the basilaminar gland pair), distinctly serrulate and often glandular leaf blade margin, and shorter inflorescences. The androecium has been incompletely or incorrectly described in the past, most likely because of its minute size (less than 1 mm in diameter). Very similar to that of *P. supraglandulosa* (Fig. 10G), it consists of an outer whorl of four (or sometimes five) stamens on short filaments, ca. 0.3 mm long, and an inner cluster of 10 to 12 sessile anthers on a globose receptacle. An annular disc, sometimes segmented, is usually evident between the outer stamens and inner anthers.

Collections from the departments of Chocó and El Valle in Colombia (*Cuatracasas 14006, 17472; Espina & Garcia 15333; Gentry & Renteria 23761, 24367; Gentry et al. 47799*) are included here but may represent yet another species in the *P. penninervia* species complex. They differ from typical collections of *P. penninervia* in having larger seeds, longer inflorescences, and laminar glands usually present on the lower leaf surface. Leaves often have a somewhat orange or reddish brown undersurface at least when dry, appearing quite distinct from the greyish or yellowish green leaves of *P. penninervia* and *P. supraglandulosa*. Collections from Pastaza province, Ecuador (*Lugo 4150, 4219, 4399*), which superficially resemble *P. loretensis*, appear to represent another taxon in the *P. penninervia* species complex.

6. PLUKENETIA POLYADENIA Muell. Arg. in Mart., Fl. bras. 11(2): 334. 1874.—*Elaeophora polyadenia* (Muell. Arg.) Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 146. 1930.—TYPE: Peru, "Maynas", *Poeppig 2385* (holotype: W, fragment at F!, photo F32544!; isotype: G!; possible isotype: NY!, labeled *Poeppig 2585*). Fig. 1B.

*Elaeophora abutifolia* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 112. fig. 9. 1925.—*Plukenetia abutifolia* (Ducke) Pax & K. Hoffm., Nat. Pflanzenfam. ed. 2. 19c: 141. 1931.—SYNTYPES: Brazil, Pará, near Belém, *Ducke, HJBR 17892* (not seen); Xingu R., *Kuhlmann, HJBR 17895* (isosyntype: U!); Tajaparú R., *Ducke, HJBR 17893* (isosyntype: P!).

*Distribution and habitat.* Widespread in the Guianas and eastern Venezuela, and in the Amazon Basin of Ecuador, northern Peru, and Brazil (Amapá, Amazonas, Pará). A canopy liana found in moist to wet, lowland or lower montane forest, sea level to 1000 m.

*Representative specimens examined.* BRAZIL. **Amapá:** Igarapé do Navio-Mazagão, *Rabelo et al. 2140* (NY). **Amazonas:** Mun. São Paulo de Olivença, basin of creek Belem, *Krukoff 8821* (F, G, K, MO, NY, P,

US); Mun. Eirunepé, Igarapé Folguedo Assahtuba, *Froes 12098* (A, F, MO, NY, US). **Pará:** Macapa, Rio Matapy, *Ducke 20619* (K, P, US).

ECUADOR. **Napo:** Río Aguarico, upriver from bridge at Aguarico, *Gentry 9717* (F, MO, NY). **Pastaza:** Comuna Shuar Amuntay, 2°31'S, 76°48'W, *Céron et al. 4319* (DAV, MO).

FRENCH GUIANA. Saül, *Mori & Gracie 18668* (K, US).

GUYANA. Camaria Falls, Cuyuni R., *Fanshawe 3383* = *FD 6947* (FDG, K, NY); Mt. Ayanganna, NE side, below talus along base, *Tillet et al. 44950* (MO, NY, US).

PERU. **Amazonas:** 1 km de La Poza, Río Santiago, *Huashikat 172* (MO). **Loreto:** Río Napo near Mazán, *Mexia 6470* (F, G, GH, K, NY, US).

SURINAM. Jodensavanne-Mapane kreek area, *Schultz 7284* (MO, U, US).

VENEZUELA. **Bolívar:** Mun. Raúl Leoni, 85 km SSE of Entre Rios, ca. 5°18'N, 63°59'W, *Aymard & Fernandez 7272* (F, MO). **Delta Amacuro:** Cerro Moco Hierro, E de Río Grande, ENE de El Palmar, *Steyermark 93082* (F, G, K, NY, US).

The species may be distinguished vegetatively by its broadly elliptic, distinctly triplinerved leaf blade that is rounded or obtuse at the base. Fruits are large, subglobose, fleshy, and indehiscent (only *P. lehmanniana* has similar fruit).

Ducke (1925, 1930) considered the species to be dioecious with dimorphic unisexual inflorescences, and noted that staminate individuals are much more common than pistillate individuals. Pistillate inflorescences are 1–3 (7) cm long, with flowers solitary at each node, while staminate inflorescences are much longer, 10–33 cm long, with flowers in one-sided (or sometimes dichasial) cymes. Of the 35 fertile collections examined, about two-thirds are staminate and one-fifth are in fruit. Only two have pistillate inflorescences as described by Ducke (*Black 52–14137*; *Ducke, HJBR 17893*), while three have bisexual inflorescences that are morphologically similar to staminate inflorescences but include either pistillate flowers (*Céron et al. 4319*, *Neill et al. 8370*) or immature fruit (*Schultz 7284*) at the basalmost nodes. This evidence suggests that individuals may be either dioecious or monoecious, or perhaps that all are monoecious, but are frequently temporally dioecious. The dioecious condition and unisexual pistillate inflorescences are unknown elsewhere in the genus. Inflorescences of all other species are typically bisexual with pistillate flowers solitary at the basalmost nodes (usually one in most species, up to ten in *P. serrata*) or occasionally staminate if the pistillate flower(s) is lacking.

A single geographically distant collection (*Ventura 522*) from Puebla, Mexico superficially resembles *P. polyadenia* in leaf shape, single knob at the petiole apex, and apparently unisexual pistillate inflorescences, but has a pistillate flower very similar to that of *P. stipellata*.

7. **Plukenetia serrata** (Vell. Conc.) L. J. Gillespie, comb. nov.—*Vigia serrata* Vell. Conc., Fl. Flum. 9: t. 127. 1832.—TYPE: Illustration t. 127 in Vell. Conc., Fl. Flum. 9. 1832.

*Fragariopsis scandens* St. Hil., Leçons bot. 426. 1840.—*Plukenetia scandens* (St. Hil.) Pax, Nat. Pflanzenfam. III. 3(5): 67. 1890.—TYPE: Brazil, *St. Hilaire 72* (holotype: P!; isotype: P!). [No collection number was cited by St. Hilaire. Of his 2 collections, 72 and 95, at P, a specimen of collection 72 has an original label quoting the protologue.]

*Accia scandens* St. Hil., Leçons bot. 499. 1840.—TYPE: not designated, probably based on one of St. Hilaire's collections at P [or perhaps a nomenclatural synonym of *F. scandens*].

*Botryanthe discolor* Klotzsch, Arch. Naturgesch. 7: 191, 204. tab. 9b. 1841.—*Fragariopsis discolor* (Klotzsch) Baill., Étude Euphorb. 498. 1858.—TYPE: Brazil, *Sellow s.n.* (holotype: B, destroyed; lectotype, here designated: P!, fragment at F!). [Klotzsch's name "Botryanthe concolor" given in the same publication was not validly published.]

*Fragariopsis polyandrus* Baill., Étude Euphorb. 498. Pl. 13, figs. 29–36. 1858.—TYPE: not designated, possibly *Guillemin 798* from Rio de Janeiro, Brazil (holotype: P!; isotypes: G!, P!).

*Fragariopsis warmingii* Muell. Arg. in Martius, Fl. bras. 11: 338. tab. 52. 1866.—*Plukenetia warmingii* (Muell. Arg.) Pax, Nat. Pflanzenfam. III. 3(5): 67. 1890.—TYPE: Brazil, Minas Gerais, near Lagos Santa, *Warming s.n.* (holotype: P!, fragment at F!; probable isotype: F!).

*Distribution and habitat.* Restricted to southeast Brazil (Bahia, Espirito Santo, Minas Gerais, Rio de Janeiro, and São Paulo). A vine or liana of wet forest, often found at the forest edge, sea level to 1000 m.

*Representative specimens examined.* BRAZIL. **Bahia:** Rodavia BA-265, ca. 25 km NW de Caatiba, *Mori et al. 9409* (DAV, NY). **Espirito Santo/Rio de Janeiro:** Itabapoana, *Samp 1001, HJBR 25979* (US). **Rio de Janeiro:** Nouvelle Fribourg (=Nova Friburgo), *Claussen 83* (G). **São Paulo:** São Paulo, grounds of the Instituto Botânico, *Davidse 10480* (NY); Pirajussára, *Gehrt 12559* (NY).

Although generally treated as a monotypic genus, *Fragariopsis* (=*Vigia*), based on androecial morphology and fleshy fruit, there appears to be no reason to exclude the species from *Plukenetia* since both characters are found within the genus. *Plukenetia polyadenia* and *P. lehmanniana* also have fleshy fruit. The androecium is unique in that the sessile anthers are widely scattered on a greatly enlarged globose receptacle, but this state may be considered derived from the more common similar state of sessile anthers densely crowded on a smaller globose receptacle (as in *P. brachybotrya* and *P. loretensis*). All anthers sessile, styles entirely connate into an obovoid column, pollen with a reticulate tectum (Gillespie, in press), and pinnately veined leaves places it in species group 2. In addition to the unusual androecium and fleshy fruit, *P. serrata* may be distinguished by the stipellate petiole apex and inflorescences with up to 10 pistillate flowers.

As Webster (in press) pointed out, the name *Vigia serrata* has precedence over *Fragariopsis scandens*, hence a new combination in *Plukenetia* must be made.

8. **Plukenetia stipellata** L. J. Gillespie, sp. nov.—TYPE: Costa Rica, Heredia, Finca la Selva, OTS Field Station on the Río Puerto Viejo, just E of junction with the Río Sarapiqui, 13 Sep 1983, *Gillespie 413* (holotype: US!; isotypes: CR!, MO!; FAA preserved material at US). Figs. 3, 4–6, 9.

A *P. volubili* L. petiolo apice stipellato, stylis brevioribus (8–10 mm), filamentis gracilibus longioribus (1–1.2 mm) at sepalis florum staminatorum plerumque 5 differt.

Monoecious twining vine; branches slender, branchlets glabrescent or sparsely puberulous. Leaves alternate, simple; stipules small, deciduous; petiole 2.5–7 cm long, sparsely puberulous; blade chartaceous, triangular-ovate or broadly triangular-ovate, 8–15 cm long, (4) 6–13 cm wide, slender-acuminate at apex with acumen 0.8–2.0 cm long, cordate at base with sinus 0.6–1.5 (2.5) cm deep, serrulate, glabrescent or sometimes sparsely puberulous below, major veins puberulous below; venation palmate, primary veins 3, secondary veins 2–3 on each side of central primary vein and 2–4 on lower side of lateral primary veins, brochidodromous, tertiary veins percurrent; quaternary veins reticulate; basilaminar glands 2, narrowly transverse-elliptic to obovate, 0.4–1.8 mm long, 1–3.2 mm wide, marginal, adaxial; laminar glands absent; pair of stipels at petiole apex between basilaminar glands, stipels conical, 0.3–1.0 mm long, pointed or rounded at apex, rarely with minute glandular knob between. Inflorescence slender racemose, (2) 6–10 (23 in fruit) cm long, bisexual, terminal on short shoots bearing 1–2 leaves or rarely axillary, axes puberulous, pistillate flower single at basal-most node, staminate flowers numerous in condensed cymes at distal nodes, cyme axes to 1 mm long; bracts triangular, 0.6–1 (1.7) mm long. Staminate pedicel 0.3–0.8 mm long, puberulous; bud broadly elliptic, 1.8–2.5 mm long, obtuse at apex; sepals (4) 5, narrowly ovate, 2–3 mm long, ca. 1 (1.5) mm wide, sparsely puberulous especially at base, valvate; corolla and disc absent; stamens 25–40 on convex receptacle ca. 0.5 mm in diameter, filaments slender, 1–1.5 mm long; pollen oblate-spheroidal, 53–60 μm in polar diameter, 58–69 μm in equatorial diameter, tricolpate, amb obtuse-triangular, colpus broad with uneven margins, tectum foveolate, surface smooth to minutely scabrate. Pistillate pedicel 2.5–5 mm long, puberulous; sepals 4, triangular or narrowly triangular, 1–1.5 mm long, acute or attenuate at apex, glabrescent; corolla and disc absent; ovary 4-locular, 1–3 mm long, 2.2–7 mm wide, puberulous, 4-winged, wings rounded, each locule uniovular; styles connate into a cylindrical column, 6–11 × 0.8–2.0 mm, sparsely puberulous, the 4 free style arms 1–2 mm long, divergent and appearing cross-shaped when mature. Fruiting pedicel 1.5–2.5 cm long; capsule 4-lobed, 1.2–2.0 × 2.3–3.2 cm, glabrous, each carpel lobe carinate with central rounded horn. Seeds lenticular, laterally compressed, 1.1–1.4 cm long, 0.3–0.5 cm wide, 0.9–1.4 cm thick, angular-circular in outline, brown with irregular dark brown patches, ecarunculate.

*Distribution and habitat.* Found from Veracruz and Chiapas, Mexico to Panama and pos-

sibly northern Colombia (see discussion below). A twining vine of disturbed sites in moist to wet forest, sea level to 1200 m.

*Representative specimens examined.* COSTA RICA. **Alajuela:** N of San Ramón, kms 15–35 of road to La Tigre and Fortuna, *Taylor et al. 4193* (MO). **Alajuela/Guanacaste:** slopes of Miravalles, above Bijagua, *Gomez et al. 19184* (MO). **Cartago:** Atirro, Turrialba, *Zamora 1306* (F, MO). **Heredia:** 1 km W of Puerto Viejo de Sarapiqui, *Jiminez 3611* (F, MO, NY). **Limón:** 29 air km W of Tortuguero, 10°30′N, 83°47′W, *Davidson et al. 6734* (F, MO, NY, US); S end of Lomas de Sierpe, NE of terminus of road from Villa Franca, 10°19′N, 83°34′W, *Grayum et al. 3511* (DAV, F, MO). **Puntarenas:** Reserva Forestal Golfo Dolce, Osa Peninsula, Rancho Quemado, ca. 15 km W of Rincón, *Hammel et al. 16933* (MO); Rincón de Osa, slopes above airport, *Liesner 2068* (MO, US).

GUATEMALA. **Alta Verapaz:** Secanquim, *Cook & Griggs 265* (US); between Secoyocté and Sepacuité, *Pittier 324* (US), *342* (BM, NY, US).

MEXICO. **Chiapas:** ca. 1 mi NE of Ruinas de Palenque, *Armbruster 78420* (DAV). **Veracruz:** Estacíon de Biologia Tropical Los Tuxtlas, San Andrés Tuxtla, *Cedillo & Calzada 56*, *MEXU 41650* (BM, F, K, MO); La Palma, Sontecomapa, Los Tuxtlas, *Sousa 2661* (US); Hidalgotitlan, 17°18′N, 94°38′W, *Vazquez et al. 1253*, *MEXU 44836* (BM, MO).

NICARAGUA. **Matagalpa:** Cerro Musún, 8 km de la Poblacion Wanawás, *Araquistain & Moreno 2360* (DAV, MO). **Río San Juan:** 1 km E of Río Sabalos, 11°2′N 84°27′W, *Moreno 23204* (MO). **Zelaya:** Monkey Point, 11°36′N, 83°39′W, *Moreno & Sandino 12112* (DAV, F, MO); Río Punta Gorda, 11°32′N, 84°05′W, *Moreno & Sandino 13085* (K, MO); ca. 3–4 km SW of Colonia Naciones Unidas on road to Colonia Nuevo Leon, ca. 11°42′N, 84°19–20′W, *Stevens et al. 5088* (F, MO).

PANAMA. **Cocle:** ca. 12 mi from Llano Grande, 8°47′N, 80°28′W, *Churchill et al. 4149* (MO). **Colón:** S of Porto Bello, along stream running into Río Buena Ventura, *Foster 2060* (F, GH, MO); along Río Guanche, 6 km S of Portobelo, *Nee & Gentry 8686* (MO). **Darién:** Cerro Pirre, valley between Pirre and next most southerly peak, *Folsom et al. 4426* (F, MO). **Los Santos:** between Los Santos and Guanare, *Woodson et al. 1201* (A, F, MO, NY). **Panamá:** 4–5 hrs walk upriver from Torti Arriba, *Folsom et al. 6845* (F, MO).

This species, widespread and moderately common in Mesoamerica, has previously been confused with *P. volubilis*, a species restricted to South America and the Lesser Antilles. Although similar to *P. volubilis* in habit and overall appearance, *P. stipellata* differs in having a pair of minute stipels at the petiole apex (Fig. 9B), a shorter stylar column (Fig. 9C), and staminate flowers having stamens with longer slender filaments and usually five sepals (Fig. 9D). The two stipel-like appendages at the petiole apex are conical in shape, either pointed or somewhat rounded at the apex and at least sometimes appear to be glandular.

Several collections from north central Venezuela appear to be morphologically intermediate between this species and *P. volubilis* and will be discussed in greater detail under the latter species. Two fruiting collections from Colombia, *Pennell 4584* from the state of Bolívar and *Duke 15375* from Chocó, have leaves with paired stipels at the petiole apex and may belong to this species. However, because of the lack of flowers it is not possible to determine whether these collections represent this species or are more similar to the intermediate population from north central Venezuela.

9. **Plukenetia supraglandulosa** L. J. Gillespie, sp. nov.—TYPE: French Guiana, Sommet Tabulaire, zone centrale, versant occidental, ca. 40 km SE de Saül, 27 Aug 1980, *Granville 3626* (holotype: US!; isotypes: CAY!, U!). Figs. 2, 7–8, 10.

*P. penninerviae* Muell. Arg. et *P. multiglandulosae* Jabl. affinis, a quibus differt inflorescentia longissima et foliis supraglandulosis glandibus numerosis dispersis.

Monoecious liana; branches slender, branchlets puberulous. Leaves alternate, simple; stipules small, deciduous; petiole 0.5–2.0 cm long, puberulous; blade chartaceous, elliptic or ovate-elliptic, 7–13 × 3–8 cm, slender-acuminate at apex with acumen 0.5–1 cm long, acute, cuneate or sometimes obtuse at base, serrulate, glabrescent except basal part of midrib puberulous, major veins and midrib sometimes sparsely puberulous below; venation pinnate, secondary veins 6–10 on each side of primary vein, distinctly brochidodromous, tertiary veins percurrent, quaternary veins reticulate; basilaminar glands 2–4 (6), circular or elliptic, 0.6–1.9 mm long, 0.5–0.7 mm wide, adaxial, arranged in pairs on either side of midrib; laminar glands circular, 0.4–0.7 mm in diameter, on both surfaces, 10–20 mostly 1–5 mm from margin below, 8–18 scattered between midrib and margin above. Inflorescence slender racemose, 2–8 cm long, bisexual, axillary, axes puberulous; pistillate flower single at base, staminate flowers numer-

ous in condensed cymes above; bracts triangular, ca. 1 mm long. Staminate pedicel 3.5–4.5 cm long, densely puberulous; bud subglobose, ca. 1 mm long or less, rounded or broadly obtuse at apex; sepals 4, elliptic, 1–1.3 mm long, acute and thickened at apex, reflexed; corolla absent; disc 4-lobed, located between outer stamen whorl and inner stamen cluster; androecium of 6–9 sessile anthers on central, shortly stipitate, globose receptacle and 4 outer stamens with filaments 0.3–0.4 mm long arising from under disc and arching upwards; pollen suboblate, 31–33 μm in polar diam., 39–45 μm in equatorial diam., tricolpate, amb obtuse-triangular, colpus broad with uneven margins, tectum reticulate, muri crenate. Pistillate pedicel 6–12 mm long, puberulous; sepals 4, triangular, ca. 1 mm long, puberulous; corolla and disc absent; ovary 4-locular, each locule uniovular, ca. 1 mm long, ca. 2 mm wide, densely puberulous, 4-winged, wings rounded; styles entirely connate into a stout-cylindrical column, ca. 1.6 × 0.6 mm, sparsely puberulous. Fruiting pedicel ca. 25 mm long; capsule 4-lobed, ca. 7 × 15 mm, sparsely puberulous, pendent, each carpel lobe with conical tubercle ca. 1 mm high. Seeds lenticular, laterally compressed, ca. 7 mm long, 4.6–4.8 mm wide, circular to broadly elliptic in outline, reddish brown with raised reticulate pattern, ecarunculate.

*Distribution and habitat.* Endemic to French Guiana and the Brazilian state of Amapá. A slender liana known from submontane forest on lateritic plateau summits at 500–800 m in French Guiana and along roadside through heavily forested hills at 70–300 m in Amapá. Flowers reported in January, August and November; fruits reported in January and August.

*Additional specimens examined.* BRAZIL. **Amapá:** Serra do Navio, along main road between Igapo Baixinho and road to Porto Terezinha, 70–300 m, *Cowan 38204* (K, NY, US).

FRENCH GUIANA: Massif du Décou Décou, E summit, *Granville 5315* (U); Mont Atachi Bacca, S of summit plateau, 12 km SE of Gobaya Soula, 3°33′N, 53°55′W, *Granville et al. 10783* (CAY, US).

The species belongs to the *P. penninervia* species complex and may be distinguished from *P. penninervia* by the leaves having numerous laminar glands scattered on both upper and lower leaf surfaces (Fig. 2), the minutely serrulate leaf margin, and the longer inflorescences, and from *P. multiglandulosa* by the scattered laminar glands on the upper leaf surface, puberulous indumentum, and longer inflorescences. While many species of *Plukenetia* have scattered laminar glands on the lower leaf surface mostly near the margin and all have one to several pairs of basilaminar glands on the upper surface, *P. supraglandulosa* is the only species to have laminar glands scattered on the upper surface.

10. PLUKENETIA VERRUCOSA Smith, Nova Acta Regiae Soc. Sci. Upsal. 6: 4. 1799.—TYPE: Surinam, *Herb. Linnaeus* (LINN, not seen, microfiche IDC 5073.1489.2!). Fig. 1D.

*Plukenetia integrifolia* Vahl, Eclog. Amer. 3: 43. 1807.—TYPE: Guyana, "Demerari", *von Rohr s.n.* (holotype: C, not seen, photo A!).

*Distribution and habitat.* Restricted to and apparently rare in Trinidad, the Guianas, and northern Amazonian Brazil (Amapá, northeast Amazonas, Pará, and Roraima). A slender twining vine found mostly in disturbed areas or forest edge of lowland wet forest.

*Representative specimens examined.* BRAZIL. **Amapa:** on lower slopes of Mt. Tipac, 3°36′N, 51°19′W, *Irwin 48796* (NY, US). **Amazonas:** Janauari, Rio Negro opposite Manaus, *Prance et al. 11255* (DAV). **Pará:** right branch of Rio Moju, *Burchell 9369* (K, NY, P). **Roraima:** Rio Branco, *Kuhlmann 252, HJBR 2996* (DAV).

FRENCH GUIANA. St. Jean du Maroni, *Benoist 893* (P); Karouany (also Maroni), *Sagot 22* (BM, G-BOIS, G-DC, K, MPU, P, U; includes several collections).

GUYANA. Camp Macaw Falls, Waini R., *Beckett 8455* (BRG, NY).

SURINAM. Nickerie R., near Awawara, *BW 893* (K, U); Voltzberg, *Pulle 221* (U).

TRINIDAD. Catham, Cedras, *Broadway, TRIN 7236* (NY).

Despite its cordiform or ovate, triplinerved leaves, this species appears to be most closely related to the neotropical species having elliptic, pinnately veined leaves. The species fits well into species group 2, being characterized by an androecium of dimorphic stamens, virtually identical to that of the *P. penninervia* species complex (Fig. 10G), styles that are entirely fused into an obovate or subglobose column (Fig. 1D) similar to that of *P. brachybotrya*, a small four-lobed capsular fruit, and pollen with a reticulate tectum (Gillespie, in press). *Plukenetia verrucosa* may be distinguished vegetatively from the other species having triplinerved or palmately

veined leaves (i.e., species group 1) by its less robust habit and thinner, narrower leaves with a stipellate petiole apex.

11. PLUKENETIA VOLUBILIS L., Sp. pl. 1192. 1753.—TYPE: West Indies, Illustration t. 13 (lower half) in Plumier, Nov. Pl. Amer. 47. 1703. Figs. 1C, 9E.

*Plukenetia peruviana* Muell. Arg., Linnaea 34: 157. 1865.—SYNTYPES: Peru, *Herb. Pavon* (G-DC!, photo F 7111!, G!); Peru, "prov. Maynas", *Poeppig 2110* (not seen).

*Plukenetia macrostyla* Ule, Verh. Bot. Vereins Prov. Brandenburg 50: 80. 1908.—TYPE: Brazil, Amazonas, Rio Juruá, near Jaburú, *Ule 5864* (isotype: G!, photo F 24573!, fragment at F!).

?*Fragariopsis paxii* Pittier, J. Wash. Acad. Sci. 19: 351. 1929.—TYPE: Venezuela, Federal District, Loma de En Medio, Valley of Puerto la Cruz, 1000 m, *Pittier 8109* (isotypes: GH!, US!) [appears to be intermediate between *P. volubilis* and *P. stipellata*; see discussion below].

*Distribution.* Found in the Lesser Antilles, Surinam, and along the northern and western edge of the Amazon basin in Venezuela (Amazonas), Colombia (Meta), Ecuador, Peru, Bolivia, and Brazil (western Amazonas). A twining vine found in disturbed areas or forest edge of moist or wet lowland forest up to 900 m.

*Representative specimens examined.* BOLIVIA. **La Paz:** Basin of Río Bopi, San Bartolome, *Krukoff 10082* (A, F, G, NY, US). **Santa Cruz:** 4 km (by air) WSW of Buena Vista, 17°28'S, 63°42'W, *Nee 35694* (MO, NY).

BRAZIL. **Amazonas:** Mun. Eirunepé, basin of the upper Jarua, *Froes 44* (US), 48 (US). **Pará:** vicinity of Pará, *Baker 153* (BM, G).

COLOMBIA. **Meta:** Cano Yerli, entre el rio Guelar y el caño Guapayita, Cordillera La Macarena, *Idrobo & Schultes 758A* (F, GH, MO, NY, US). **Putumayo:** Puerto Limon, cultivated, *Plowman 2191* (ECON).

DOMINICA. Rosehill, *Eggers 580* (G, GH).

ECUADOR. **Napo:** 4 km S de Puerto Napo en el Río Napo, *Dodson et al. 14926* (K, MO, NY); Limoncocha, *Zarucchi 2369* (GH, MO, US), *2378* (DAV, GH, US).

GRENADA. Concord R., *Eggers 6470* (P, US).

MARTINIQUE. Near Lamentin, *Hahn 1278* (P).

PERU. **Amazonas:** Lugar Huampami, *Ancuash 248* (GH, MO). **Cuzco:** Atalaya, Kosáipata, prov. Pancastambo, *Vargas 13994* (US). **Junín:** Satipo, *Woytkowski 5891* (MO, US). **Loreto:** Mishuyacu, near Iquitos, *Klug 1438* (F, US). **Madre de Dios:** Piáipiái, Defensa, Prov. Manu, *Vargas 11616* (US). **San Martín:** Juin Jui, alto Río Huallaga, *Klug 3901* (F, K, MO, US).

ST. VINCENT. In forest, *Smith & Smith 422* (BM, GH, NY, US).

SURINAM. Valley of West River, 2–5 km SW of Juliana Top, *Irwin et al. 54897* (F, GH, MO, NY, U, US).

VENEZUELA. **Amazonas:** 0–1 km S of Río Mawarinuma, 3 km by air E of Cerro de la Neblina Base Camp, 0°50'N, 66°09'W, *Liesner 16197* (DAV, MO, NY).

This species may be distinguished from the closely related species, *P. stipellata*, by a single glandular knob at the petiole apex, longer stylar column (Fig. 1C), and staminate flowers with short conical filaments and four sepals (Fig. 9E). The stylar column is the longest of any species of *Plukenetia* and may attain a length of 3 cm.

An isolated population (represented by the collections, *Agostini & Fariñas 54* and *Steyermark 89966*) in the coastal mountains of north central Venezuela (Estado Miranda and Distrito Federal) appears to be morphologically intermediate between *P. volubilis* and *P. stipellata*. Although identical to *P. volubilis* in staminate flower morphology including sepal number, stamen number, and filament size and shape, these collections have leaves with paired stipels at the petiole apex typical of *P. stipellata*. Stylar column length is intermediate between the two species (10–15 mm long). The type collection of *Fragariopsis paxii, Pittier 8109*, appears to belong to this population. Pittier considered his new species to belong "without any possible doubt" to *Fragariopsis*, presumably on the basis of the paired stipels (unknown in *Plukenetia* at that time) and the stamens which he misinterpreted as lacking filaments. The style was incorrectly described as 5–6 mm in length, much shorter than the stylar columns of either *P. stipellata* or *P. volubilis*. Pittier most likely examined specimens having immature or incomplete flowers such as the specimen at US which has only a single pistillate flower with a stylar column broken near its base. However, the specimen at GH includes pistillate flowers with stylar columns 14–15 mm long, congruent with other collections of this morphologically intermediate population.

The greatest degree of variation in *P. volubilis* is found in collections from the eastern slopes of the Andes bordering the Amazon basin in Peru. While the majority of collections may be considered as typical of the species, there are a number of morphologically unusual ones. Two

collections (*Klug 3846, 3901*) from San Martín, Peru have flowers with somewhat longer (0.8 mm) slender-conical filaments; *Klug 3846* also has flowers with style arms 3–4 mm long rather than the typical length of 1–2 mm. Collections from Cuzco, Junín, and Pasco, Peru at 1600–2100 m, elevations much higher than either *P. volubilis* or *P. polyadenia*, the only other members of species group 1 known from Peru, may represent a distinct species (*Gentry & Smith 35906, Solomon 3166, Woytkowski 6670*). While labeled *P. volubilis*, the collections most closely resemble *P. stipellata* in floral morphology and *P. lehmanniana* in aspect including the more robust denser inflorescences with larger flowers.

Several collections have unusually large capsules with five or six carpels (*Killip & Smith 29927, McDaniel & Rimachi 30269, Vargas 13994*, and *Vásquez & Jaramillo 6167* from Peru, *Mexia 7265* from Ecuador, and *Plowman 2191* from Colombia). Three of these collections are recorded as cultivated, while labels of four mention that the seeds are edible and are eaten roasted like peanuts (several of the common names recorded, e.g., sacha-inchik and sacha mani, translate as wild peanut). Thus the higher than normal carpel number appears to be a character selected for under cultivation. Frequently correlated with a carpel number of five or six is a more prominently serrate leaf margin, as opposed to the typical serrulate condition.

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