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A Revision of Paleotropical *Plukenetia* (Euphorbiaceae) Including Two New Species from Madagascar

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ABSTRACT. A revision of the seven paleotropical species of *Plukenetia* (Euphorbiaceae) is given. Three sections or species groups are recognized. Two genera, *Tetracarpidium* (synonym *Angostylidium*) and *Pterococcus*, are treated here as sections of *Plukenetia*. The monotypic *P.* sect. *Angostylidium* includes the African species *P. conophora*, while *P.* sect. *Hedraiostylus* (synonym *P.* sect. *Pterococcus*) comprises two African species (*P. africana* and *P. procumbens*) and one Asian species (*P. corniculata*). A third species group restricted to Madagascar is distinguished by an androecium of sessile anthers on an elongate receptacle, and comprises three species, two described here. ***Plukenetia decidua***, from southeastern Madagascar, is close to *P. madagascariensis* and shares styles partly fused into a cylindrical column, but differs in its narrower ovate or triangular-ovate leaf blades, smaller eglandular bracts, racemes with flowers single per node, and fewer anthers on a shorter ellipsoid receptacle. ***Plukenetia ankaranensis*** from northern Madagasar is distinguished from the previous two species by its styles entirely fused into an enlarged obovate stylar column. A key to the seven paleotropical species is provided and their relationship to neotropical species is discussed.

KEYWORDS: *Pterococcus*, taxonomic revision, *Tetracarpidium*.

Plukenetia L. (Euphorbiaceae s.s.) is a pantropical genus of 19 species belonging to tribe Plukenetieae of subfamily Acalyphoideae. The genus is unusual in the Euphorbiaceae for its 4-carpellate ovary and vine or liana habit. Twelve species are known from the Neotropics, and a synopsis of eleven of these was previously presented (Gillespie 1993). In the same year, one new species, *P. carabiasiae* Jiménez, was described from Mexico (Jiménez 1993). A revision of the seven paleotropical species, including two new species from Madagascar, is presented here. One of these new species, *P. ankaranensis*, was first collected by the author during a field trip to Massif Ankarana in northern Madagascar.

Plukenetia species are twining vines, lianas, or rarely sprawling perennial herbs, found in tropical wet forest to seasonally dry forest or scrub. Excellent field identification characters for the genus are the presence of distinct paired, circular or elliptic basilaminar glands on the adaxial surface of the leaf blade and 4-parted fruit.

Taxonomic History and Generic Circumscription. *Plukenetia* is considered here in the broad sense to comprise all members of tribe Plukenetieae having a 4-carpellate ovary (Gillespie 1993). This includes the segregate genera *Apodandra* Pax & K. Hoffm., *Eleutherostigma* Pax & K. Hoffm., *Fragariopsis* A. St. Hil., *Pterococcus* Hassk., and *Tetracarpidium* Pax [syn. *Angostylidium* (Müll.Arg.) Pax & K. Hoffm.], but excludes the 3-carpellate genus *Romanoa* Trev. St. Léon (syn. *Anabaena* Adr. Juss.). This circumscription, with minor exceptions, follows closely that of the major 19th century works on Euphorbiaceae (Baillon 1858; Müller 1866; Bentham 1880; Pax 1890). In contrast, Pax and Hoffmann (1919, 1931), in the most recent revision of *Plukenetia* and tribe Plukenetieae, used a narrow delimitation of the genus. They elevated two paleotropical sections of *Plukenetia* to generic rank (*Angostylidium* and *Pterococcus*), described two new neotropical genera (*Apodandra* and *Eleutherostigma*), and recognized the neotropical genus *Fragariopsis* as distinct (sometimes also treated as a section of *Plukenetia*). A more detailed history of the taxonomy of *Plukenetia* and its segregate genera, particularly the neotropical ones, is described in Gillespie (1993, 1994).

Pax and Hoffmann (1919, 1931) treated the four paleotropical species of *Plukenetia* s.l. known at that time in *Angostylidium* (as *Tetracarpidium* in 1931) and *Pterococcus*. All of these species had originally been described in *Plukenetia*. Leandri (1938) described a fifth paleotropical species from Madagascar, placing it provisionally in *Plukenetia* as *P. madagascariensis* Léandri, but mentioned that it is very near to *Tetracarpidium*. Including this species in *Plukenetia* s.s. would have been a large range extension for the then narrowly defined neotropical genus. This treatment of three genera in the Palaeotropics, *Tetracarpidium* (syn. *Angostylidium*), *Plukenetia s.s.*, and *Pterococcus*, has been largely followed to the present day (e.g., Airy-Shaw 1971, 1975, 1981, 1982, 1983; Dyer 1975; Grierson & Long 1987; Radcliffe-Smith 1996; Govaerts et al. 2000).

Pax and Hoffmann's (1919, 1931) treatment of the *Plukenetia* complex was first challenged by Croizat (1941), and more recently by Webster

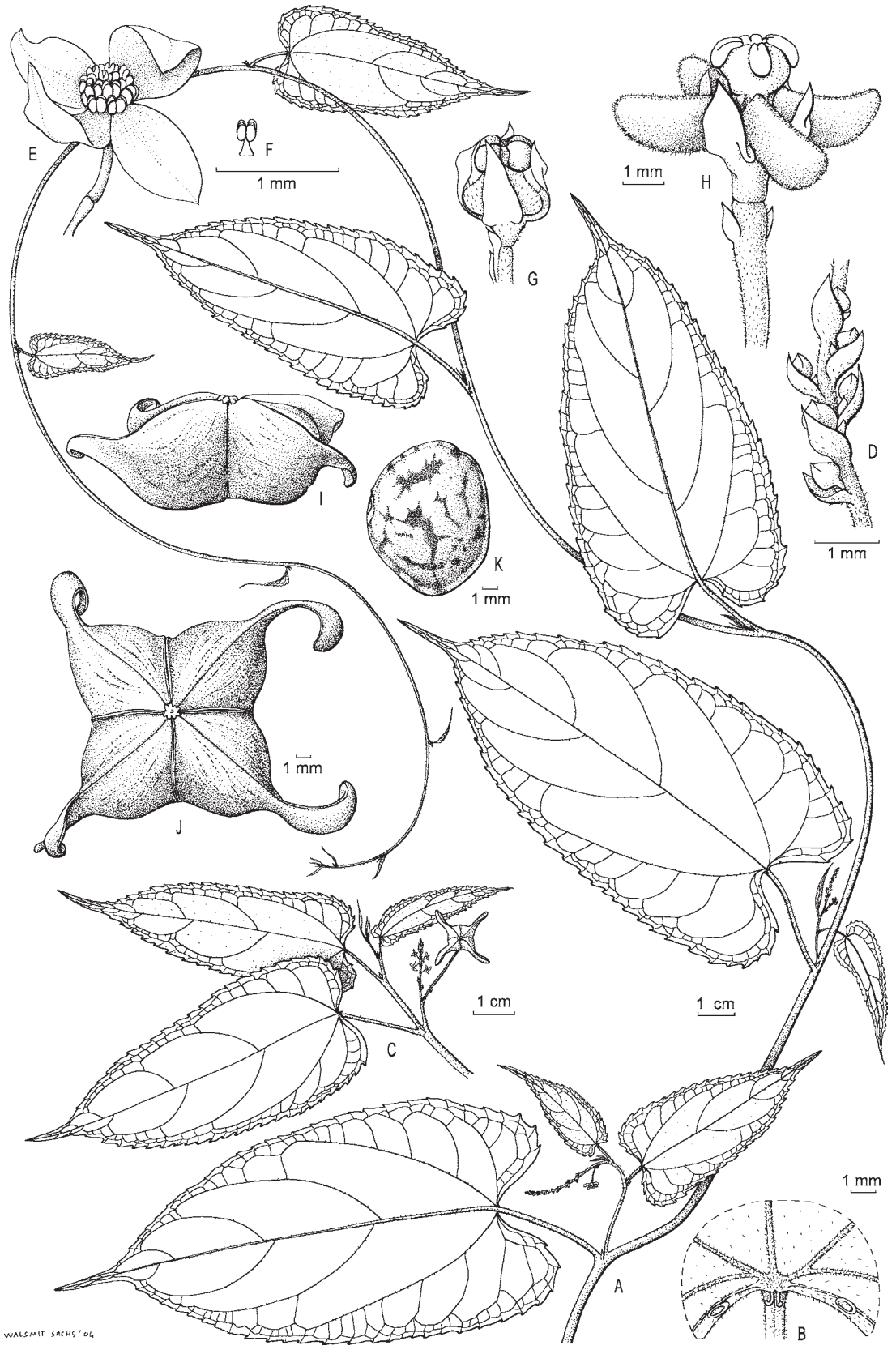
(1975, 1994) and Gillespie (1993, 1994). Croizat considered *Pterococcus* as part of *Plukenetia* because he could find no differences to separate the two genera. Croizat also remarked that the winged ovaries considered diagnostic for *Pterococcus* could be found in *Plukenetia* s.s. Likewise, he did not consider *Angostylidium* (= *Tetracarpidium*) as a distinct genus, and pointed out that Pax and Hoffmann (1919), although recognizing the genus, also considered it little distinct from *Plukenetia*. Webster (1975, 1994) included both *Tetracarpidium* and *Pterococcus* as synonyms under *Plukenetia*, a view followed by Gillespie (1993, 1994) and Radcliffe-Smith (2001).

Pterococcus was described by Hasskarl (1842) for the single species *Plukenetia corniculata* Sm. and named after its conspicuously 4-winged capsule (Figs. 1I, J). Subsequently, the genus was treated mostly as a section of *Plukenetia*, but its circumscription was controversial. Baillon (1858) included only *P. corniculata* in the genus (which he called *Hedraiostylus* Hassk.) and considered *P. africana* Sond. as a member of *Plukenetia* s.s., while Müller (1866) included *P. corniculata*, *P. africana*, and the newly described species *P. hastata* Müll.Arg. (= *P. africana*) in *P.* sect. *Hedraiostylus* (Hassk.) Müll.Arg. Bentham (1880) expanded the circumscription of *P.* sect. *Pterococcus* (Hassk.) Benth. & Hook. to comprise, in addition to these three species, two neotropical species, *P. penninervia* Müll.Arg. and *P. verrucosa* Sm., a treatment followed by Pax (1890). In 1919 Pax and Hoffmann resurrected the genus *Pterococcus*, and considered it to comprise *P. corniculata*, *P. africana* (including *P. hastata*), and the recently described species *P. procumbens* Prain.

Pax and Hoffmann (1919) characterized *Pterococcus* based on both style morphology and presence of wings on the ovaries. Likewise, Airy-Shaw (1975) considered the genus to be ''closely related to *Plukenetia*, differing principally in the very short thick stylar column and in the conspicuously 4-winged or 4-horned capsule.'' While *P. corniculata* does have a conspicuously four-winged capsule (Figs. 1I, J), *P. africana* has a capsule with four shorter wings and *P. procumbens* a capsule with four small tubercles, the latter similar to many neotropical species including *P. penninervia*, *P. supraglandulosa* L.J. Gillespie, and *P. verrucosa* (Gillespie 1993, Figs. 1D, 10I). Although not as highly developed as in *P. corniculata*, distinctly 4-winged ovaries and fruit are also found in Madagascan and neotropical species of *Plukenetia* (e.g., *P. ankaranensis*, Figs. 2E, F, and *P. loretensis* Ule). Styles of *Pterococcus* were described by Pax and Hoffmann (1919) as connate into a short thick column with sessile stigmas, as distinct from styles connate into an urceolate or cylindrical column with free arms short or absent (*Angostylidium*, *Apodandra*, *Fragariopsis*, and *Plukenetia* s.s.) or styles free above (*Eleutherostigma*). In fact, styles are not uniform within *Pterococcus*, but vary from completely connate into a very short, stout stylar column (*P. corniculata*, Figs. 1G, H) to partly connate into a short, narrower, cylindrical stylar column with free recurved arms (*P. procumbens*). The latter species does not key out under *Pterococcus* in Pax and Hoffmann's (1919) key, but instead under *Plukenetia*. Therefore, neither the style nor winged ovary characters used by Pax and Hoffmann (1919) to distinguish the genus *Pterococcus* appear to be justified.

The only character that could be used to separate *Pterococcus* from other members of *Plukenetia* s.l. is style length, with *Pterococcus* having styles shorter than or equal in length to the ovary (Figs. 1G, H). All other *Plukenetia* s.l. (except some collections of *P. brachybotrya* Müll.Arg.) have styles longer than the ovary (Figs. 2E, 3B, D, G, 4F; Gillespie 1993: Figs. 1, 9C, 10H). Given the extreme variablity of style morphology (size, shape, and degree of connation) in *Plukenetia* s.l. (Gillespie 1993), distinguishing a genus based only on style size does not seem justified. Nevertheless, the three species of *Pterococcus* appear to form a natural group, which is recognized here as *P.* sect. *Hedraiostylus* (see discussion under this section).

Plukenetia sect. *Angostylidium* Müll.Arg. was described by Müller (1864) for his new species *P. conophora*, and was subsequently consistently recognized as a monotypic section (e.g., Bentham 1880; Pax 1890). In 1919 Pax and Hoffmann raised the section to generic rank as *Angostylidium*, but soon after Hutchinson and Dalziel (1928) correctly recognized that *Tetracarpidium* has priority over *Angostylidium*, a treatment later followed by Pax and Hoffmann (1931). Pax and Hoffmann (1919, 1931) distinguished their monotypic genus from *Plukenetia s.s.* based on its high stamen number (~40 versus 12–30) and presence of intrastaminal disc segments, but also considered it to be little distinct from the latter. Neither character can be used to separate these two genera. Stamen number was found to range from 25 to 40 in *P. conophora* Müll.Arg, and some *Plukenetia* s.s. species have more than 30 stamens (e.g., *P. stipellata* L.J. Gillespie has 25–40 stamens, Gillespie 1993: Fig. 9D; *P. madagascariensis* has 35–60+ stamens). While species of *Plukenetia* s.s. either lack a staminate disc or have an annular disc (*P. penninervia* species complex, Gillespie 1993: Fig. 10G), intrastaminal disc segments similar to those of *Tetracarpidium* are present in the neotropical species *P. lehmanniana*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(Pax & K. Hoffm.) Huft & L.J. Gillespie (previously recognized as the monotypic genus *Eleutherostigma*). When considered in the context of *Plukenetia* worldwide, neither *Tetracarpidium* nor *Pterococcus* can be maintained as distinct genera.

Species Relationships. Among paleotropical *Plukenetia*, there are three well delineated species groups. *Plukenetia* sect. *Hedraiostylus* comprises two southern African species, *P. africana* and *P. procumbens*, and the only known Asian species, *P. corniculata*. The second group, *P.* sect. *Angostylidium*, comprises the single species *P. conophora* of tropical central and west Africa. The third species group comprises three species endemic to seasonally dry areas of Madagascar, *P. ankaranensis*, *P. decidua*, and *P. madagascariensis*.

Paleotropical species do not form a group distinct from neotropical species, and do not appear to share any unique characters. For the most part the three paleotropical species groups appear to have closer affinites to neotropical groups than to each other, and are linked morphologically via neotropical species.

The precise relationship of these three paleotropical species groups to the two neotropical species groups described previously (Gillespie 1993) is not entirely clear. All paleotropical species share three-nerved to weakly palmate leaves, foveolate pollen, and the lack of scattered laminar glands on the leaf abaxial surface (rarely present in two species) with *P.* sect. *Plukenetia* (= neotropical species group 1, Gillespie 1993). In addition, *P.* sect. *Angostylidum* also shares stamens with filaments, styles partly connate into a cylindrical column, and large fruit, and in fact seems to be little differentiated from *P.* sect. *Plukenetia*. In contrast, the other two paleotropical species groups share characters with both neotropical species groups. *Plukenetia* sect. *Hedraiostylus* shares a similar androecium of all stamens with filaments with *P.* sect. *Plukenetia*, and small capsules and small lenticular seeds with neotropical species group 2. On the other hand, the Madagascan species group shares an androecium of sessile anthers with species group 2, and medium-sized fruit and subglobose seeds with *P.* sect. *Plukenetia*.

Similar character trends are seen in both the Old and New Worlds, such as the trends toward entirely fused styles, winged ovaries, sessile anthers, and highly expanded staminate receptacles (characters polarized using *Romanoa* as sister group, Gillespie 1993). Some of these shared characters appear to be shared due to common ancestry, while others may represent parallel evolution. For example, the character trend from partly to entirely fused styles occurs within both the Madagascan species group and *P.* sect. *Hedraiostylus* (although less pronounced in the latter), while in the Neotropics style fusion distinguishes the two neotropical groups, with *P.* sect. *Plukenetia* having styles partly fused and species group 2 having styles entirely fused (Gillespie 1993). The presence of both states in two morphologically distinct species groups and the derived state characterizing a third group suggests that entirely fused styles arose independently at least twice and possibly three times. In contrast, the long, partly fused style of the African *P.* sect. *Angostylidium* is suggested to be a plesiomorphic character shared with *P.* sect. *Plukenetia* via common ancestry based on a close similarity in overall morphology.

Detailed discussions of species relationships and morphological character evolution, and a revised sectional classification will await the completion of molecular and phylogenetic analyses (Gillespie, work in progress). In the meantime, the existing subgeneric classification will be maintained for the paleotropical species.

Taxonomic Characters. Paleotropical species of *Plukenetia* may be distinguished by floral, fruit, and leaf characters similar to those used in characterizing neotropical species (Gillespie 1993), with the exception of leaf architecture and pollen morphology. As in the neotropics, floral and fruit morphology is surprisingly diverse. Useful staminate flower characters include presence of filaments and disc, and receptacle shape. Style morphology and size vary considerably, with styles ranging from partly to entirely fused, and the stylar columns sometimes enlargened into a variety of shapes. Fruits range from small dehiscent capsules to large indehiscent fruit, and usually have a variously shaped protuberance (wing, horn, tubercle) on each carpel. Useful foliar characters include blade shape and size, presence of stipels, and number, size, and position of basilaminar glands.

Leaf architecture and pollen morphology, both useful in characterizing the two main neotropical species groups, are insufficiently variable to distin-

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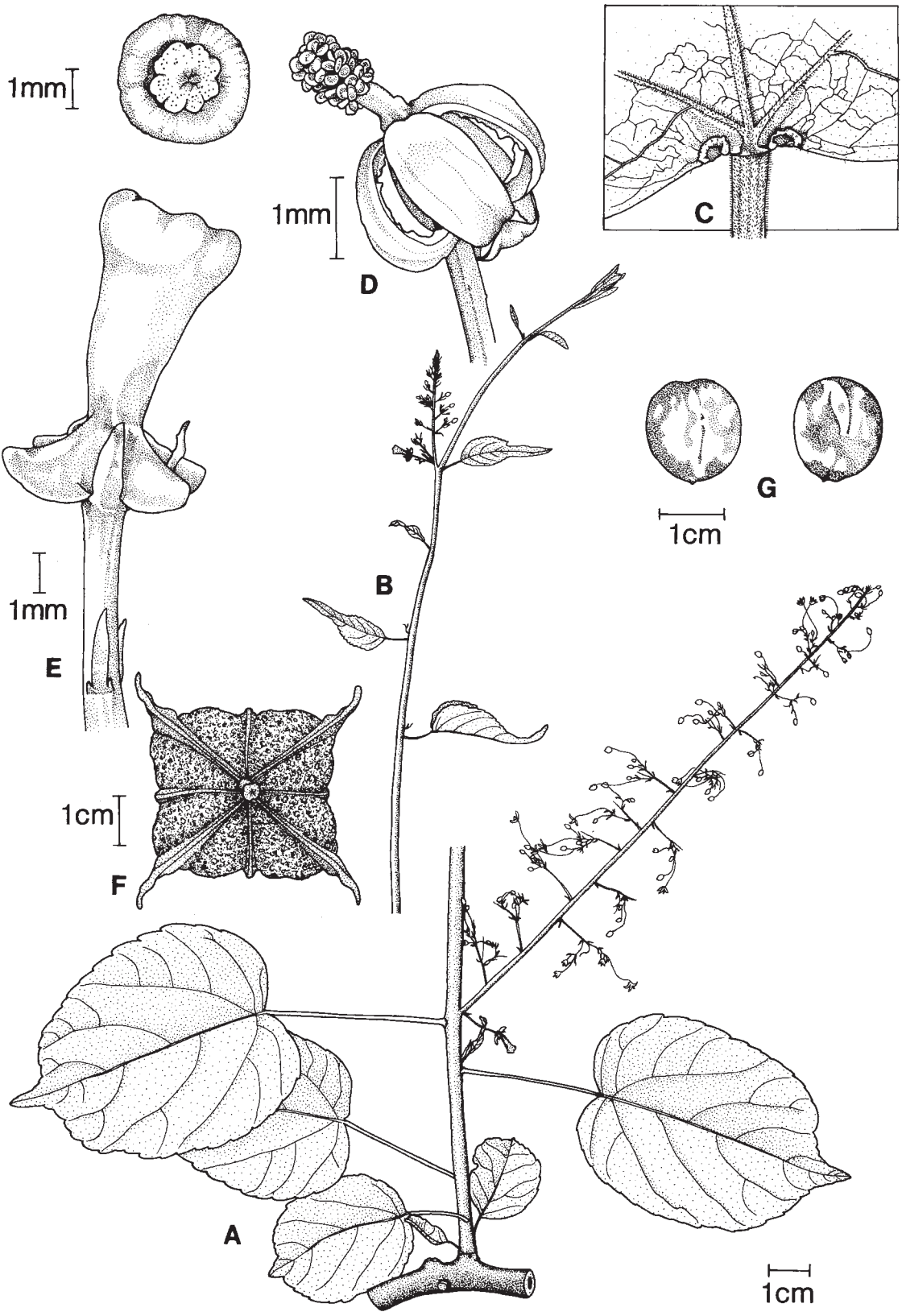
FIG. 1. *Plukenetia corniculata*. A. Twining stem with mature leaves and inflorescences. B. Close-up of leaf blade base showing paired basilaminar glands and stipels. C. Branch showing leaf-opposed inflorescence with immature fruit and staminate flowers. D. Part of inflorescence with staminate flower buds. E. Staminate flower. F. Stamen. G. Young pistillate flower. H. Pistillate flower in post anthesis stage. I. Capsule, side view. J. Capsule, top view. K. Seed, side view. A, B, D, H based on *Brink 5771*; C on *Koorders 41509*; E, F on *Chin See Chung 2712*; G on *Lorzing 7821*; I–K on *Meijer 7309*. Drawing by Anita Walsmit Sachs, used with permission from the Nationaal Herbarium Nederland.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guish among paleotropical species. Paleotropical species share medium-sized pollen grains (equatorial axis 35–51 μm long) with a foveolate exine (Gillespie 1994, and results presented here), and leaves with three-nerved to weakly palmate venation.

Paleotropical species appear to be reasonably well defined, in contrast to several neotropical species complexes, such as the poorly understood *P. penninervia* and *P. brachybotrya* complexes in the Andean and Amazonian regions (Gillespie 1993).

Taxonomic Treatment

PLUKENETIA L., Sp. Pl. 1192. 1753.—TYPE: *Plukenetia volubilis* L.

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

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

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

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

Sajorium Endl., Gen. Pl. Suppl. 3: 98. 1843.—TYPE: *Sajorium corniculatum* (Sm.) Dietr. [= *Plukenetia corniculata* Sm.]

Tetracarpidium Pax in Engl., Bot. Jarhb. Syst. 26: 329. 1899.—TYPE: *Tetracarpidium staudtii* Pax [= *Plukenetia conophora* Müll.Arg.]

Pseudotragia Pax in Engl., Bull. Herb. Boissier, ser. 2, 8: 635. 1908.—TYPE: *Pseudotragia* scandens Pax [= *Plukenetia africana* Sond.] (according to Webster, 1994).

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

Angostylidum (Müll.Arg.) Pax & K. Hoffm., Pflanzenr. IV.147.IX (Heft 68): 17. 1919.—TYPE: *Angostylidum conophorum* (Müll.Arg.) Pax & K. Hoffm. [= *Plukenetia conophora* Müll.Arg.]

Apodandra Pax & K. Hoffm., Pflanzenr. IV.147.IX (Heft 68): 20. 1919.—TYPE: *Apodandra loretensis* (Ule) Pax & K. Hoffm. [= *Plukenetia loretensis* Ule] (according to Webster 1994).

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

Lianas, vines, or rarely perennial herbs (*P. procumbens*), monoecious or rarely dioecious; latex absent; stems twining, sometimes initially erect, or rarely procumbent and sprawling. **Leaves** simple, alternate, evergreen or deciduous, petiolate; stipules small, deciduous; blade chartaceous, pinnately, palmately or 3-veined, margins subentire to serrulate or rarely serrate, often with small or minute glandular setae; pair of stipels or small knob sometimes present at petiole-blade junction; 1–6(–10) pairs of flat, usually conspicuous basilaminar glands present near base on blade adaxial surface; scattered smaller laminar glands sometimes present on abaxial surface, usually near margin, rarely present on adaxial surface (only in *P. supraglandulosa*). **Inflorescence** a racemose thyrse or rarely a raceme, axillary or terminal, bisexual with pistillate flower(s) at base and staminate flowers above, or rarely unisexual; flowers in condensed cymules, rarely in lax cymes, or single per node; bracts triangular, small, eglandular or rarely larger and biglandular (*P. madagascariensis*). **Staminate flowers** small, typically green, greenish yellow or cream; pedicels present, usually articulated (comprising cyme axis plus true pedicel); sepals 4 or 5, valvate; petals absent; glandular disc absent or present, interstaminal, segmented or annular; stamens 8 to ~60, free, on convex, subglobose, or elongate receptacle; filaments short to elongate or anthers sessile; pistillode absent; pollen tricolpate, suboblate to oblate-spheroidal, amb obtuse-triangular to subcircular, angulaperturate, exine tectate-perforate, tectum foveolate to reticulate. **Pistillate flowers** pedicellate; sepals 4; petals and disc absent; ovary 4-locular with locules uniovulate, 4-angled to deeply 4-lobed, each angle or lobe carinate and/or with a tubercle, horn, or laterally compressed wing; styles partly to completely connate, column cylindrical to globose or obovoid, free style arms absent or present, entire to obscurely bifid. **Fruit** a 4-seeded capsule (usually schizocarpous) or berry, deeply 4-lobed to subglobose, each carpel carinate and/or with central tubercle or wing.

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FIG. 2. *Plukenetia ankaranensis* sp. nov. A. Branch with mature leaves and inflorescence. B. New shoot with young inflorescence. C. Closeup of leaf showing glands at base of blade. D. Staminate flower. E. Pistillate flower, with view of apex shown above. F. Capsule. G. Seed, ventral view (left), lateral view (right). A, B, D, E based on *Gillespie 4074*; C on *Gillespie 4088*; F, G on *Gillespie 4076*.

Seeds subglobose, ovoid, or lenticular and then laterally compressed, ecarunculate, surface smooth, rough, or verrucate; outer seed coat (testa) thin, persistent or not.

KEY TO THE PALEOTROPICAL SPECIES OF *PLUKENETIA*

1. Fruit ≥ 5 cm wide; seeds broadly ovoid, > 2.5 cm long; staminate disc segments numerous, slender, interstaminal; stamens 25–40 with filaments on small subglobose receptacle; inflorescence axillary; styles 4–8 mm long, longer than the ovary, mostly connate into a thick cylindrical column, free style arms short, conspicuously dilated and spreading; tropical Africa (*P.* sect. *Angostylidium*) . . . . . 1. *P. conophora*
1. Fruit < 4 cm wide; seeds lenticular, broadly ellipsoid, or subglobose, < 2 cm long; staminate disc absent; stamens 8–60, if > 20 then anthers sessile on elongate receptacle; inflorescence position various; styles not as above. . . . . .
   2. Androecium of sessile anthers on prominent elongate receptacle; styles > 3 mm long, longer than the ovary; capsules 2–4 cm wide; seeds broadly ellipsoid to subglobose, 1.3–1.8 cm long (capsule and seeds unknown for *P. madagascariensis*); inflorescence position various; Madagascar (Madagascan species group). . . . . .
      3. Styles entirely connate, < 6 mm long, stylar column obconic or obovoid, free style arms absent; androecium ≤ 1 mm long, anthers 15–20; inflorescence a thryse, terminal and appearing leaf-opposed, staminate flowers in distinct cymules; glandular knobs absent at petiole apex . . . . . 5. *P. ankaranensis*
      3. Styles partly connate (~1/2 of length), > 7 mm long, stylar column cylindrical, free style arms slender, tapered; androecium > 1.5 mm long, anthers 18–60+; inflorescence a very narrow thyrse or raceme, axillary or terminal, staminate flowers single per node or in condensed cymules; glandular knobs 1–2 at petiole apex, sometimes minute. . . . . .
         4. Inflorescence a terminal raceme, flowers single per node; bracts triangular, ≤ 2 mm long, epetiolate, eglandular; androecium 1.6–1.8 mm long, anthers 18–30 on oblong-ellipsoid receptacle; leaf blades triangular-ovate or ovate . . . . . 7. *P. decidua*
         4. Inflorescence an axillary thryse, flowers in condensed cymules; bracts lanceolate, 3–8 mm long, usually petiolate and biglandular; androecium 3–4 mm long, anthers 35–60+ on narrowly conical receptacle; leaf blades broadly ovate or orbicular. . . . . 6. *P. madagascariensis*
   2. Androecium of stamens with filaments on small convex to globose receptacle; styles < 2 mm long, shorter than or length equal to the ovary; capsules ≤ 2 cm wide; seeds broadly lenticular, laterally compressed, < 1.2 cm long; inflorescence terminal, appearing leaf-opposed; southern Africa and southeast Asia (*P.* sect. *Hedraiostylus*). . . .
      5. Petioles > (1–)3 cm long; leaf blade > (2–)4 cm wide, deeply cordate at base, with 2 conspicuous basilaminar glands and 2 stipels at base; capsule with strap-shaped wing 6–12 mm long on each carpel lobe; Asia . . . . . 3. *P. corniculata*
      5. Petioles < 1 cm long; leaf blade < 3.5 cm wide, obtuse to truncate, hastate, or rarely sagittate at base, with basilaminar glands 2–12(–20), sometimes minute or absent, and stipels minute or absent; capsule with tubercle or wing ≤ 3 mm long on each carpel lobe; southern Africa. . . . . .
         6. Leaf blade elliptic or ovate (L/W 0.6–0.8), 2–4.5 cm long, obtuse or rounded at base; basilaminar glands 2–12(–20) . . . . . 4. *P. procumbens*
         6. Leaf blade narrowly triangular, lanceolate or linear-lanceolate [L/W 0.05–0.4 (–0.6)], 3–8 cm long, often hastate at base; basilaminar glands 2, often minute or absent . . . . . 2. *P. africana*

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

1. PLUKENETIA CONOPHORA Müll.Arg., Flora 47: 530. 1864. *Angostylidium conophorum* (Müll.Arg.) Pax & K. Hoffm., Pflanzenr. IV.147.IX.(-Heft 68): 17. 1919. *Tetracarpidium conophorum* (Müll.Arg.) Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 307. 1928.—TYPE: ''Cameroon River'' [Cameroun?], *Mann 2202* (lectotype, here designated: K! [sheet annotated as ''originalis'' by Müller Arg.]; isolectotypes: K-2 sheets!).

Tetracarpidium staudtii Pax, Bot. Jahrb. Syst. 26: 329. 1899.—TYPE: Cameroun. Station Johann-Albrechtshöhe, 15 Jan 1897, *Staudt 802* (holotype: B, destroyed, illustration at K!, fragment of holotype at K!; isotypes: BM!, MO!).

Mallotus preussii Pax, Bot. Jahrb. Syst. 23: 525. 1897. *Cleidion preussii* Baker, Kew Bull. 143. 1910.—TYPE: Cameroun, Barombistation, 25 Aug 1890, *Preuss 420* (holotype: B, destroyed, illustration at K!; isotypes: BM!, K!).

Cleidion mannii Baker, Kew Bull. 58. 1910.—TYPE: ''Upper Guinea, Cameroon River,'' *Mann 1202* (holotype: K!).

Monoecious (functionally dioecious ?) liana, to ~30 m high, trunk to 14+ cm in diam; stems sometimes twining, glabrescent. Stipules triangular, ~0.5 mm long. **Leaves** evergreen; petioles (1.5–)3–6 cm long, glabrous or very sparsely pubescent with apex pubescent; blades elliptic or ovate, 5–12 × 3.5–9 cm, chartaceous, mostly glabrous with base pubescent and major veins very sparsely pubescent, acute to obtuse at apex with acumen 0.5–1 cm long, broadly obtuse, rounded, or rarely shallowly cordate at base, margins serrulate or crenulate-serrulate; venation 3-nerved at base, sometimes weakly palmate, secondary veins mostly brochidodromous or sometimes semi-craspedodromous, 3–4 on each side of midrib, tertiary veins percurrent or

FIG. 3. *Plukenetia ankaranensis* and *P. madagascariensis*. A–D. *P. ankaranensis*. A. Liana climbing up small tree on eroded limestone pavement. B. Flowering branch showing single pistillate flower at base of inflorescence and staminate flowers in bud above. C. Liana with inflorescences. D. Close-up of short inflorescence with two basal pistillate flowers and open staminate flowers. E–G. *P. madagascariensis*. E. Liana in dry forest. F. Vegetative branch. G. Inflorescences; the basal part of three inflorescences is shown, the lower-most one has a single basal pistillate flower, the one on the upper left shows the staminate flower buds, and the one on the right has an open staminate flower. A, D. *Gillespie 4076*; B. *Gillespie 4074*; C. *Gillespie 4088*; E–F. *Gillespie 4125*; G. *Andrianjafy et al. 1648*. Scale bar in B, F = 2 cm; bar in D = 5 mm; bar in G = 1 cm.

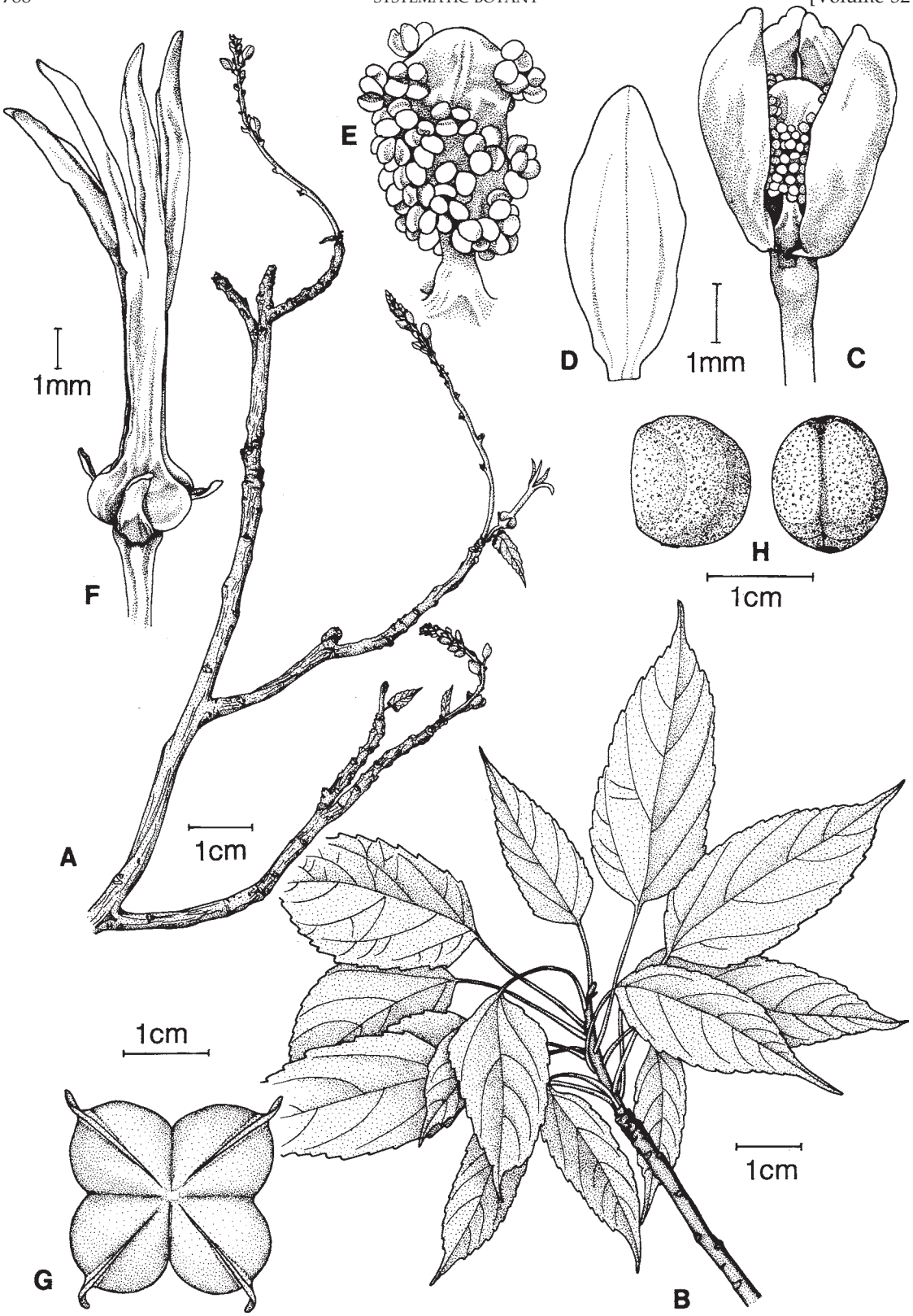

FIG. 4. *Plukenetia decidua* sp. nov. A. Branch with inflorescences. B. Branch with leaves. C. Staminate flower. D. Staminate sepal. E. Androecium. F. Pistillate flower. G. Capsule. H. Seed, lateral view (left), ventral view (right). A, C–F based on *Capuron SF 18682*; B on *Capuron SF 27952*; G–H on *Decary 3253*.

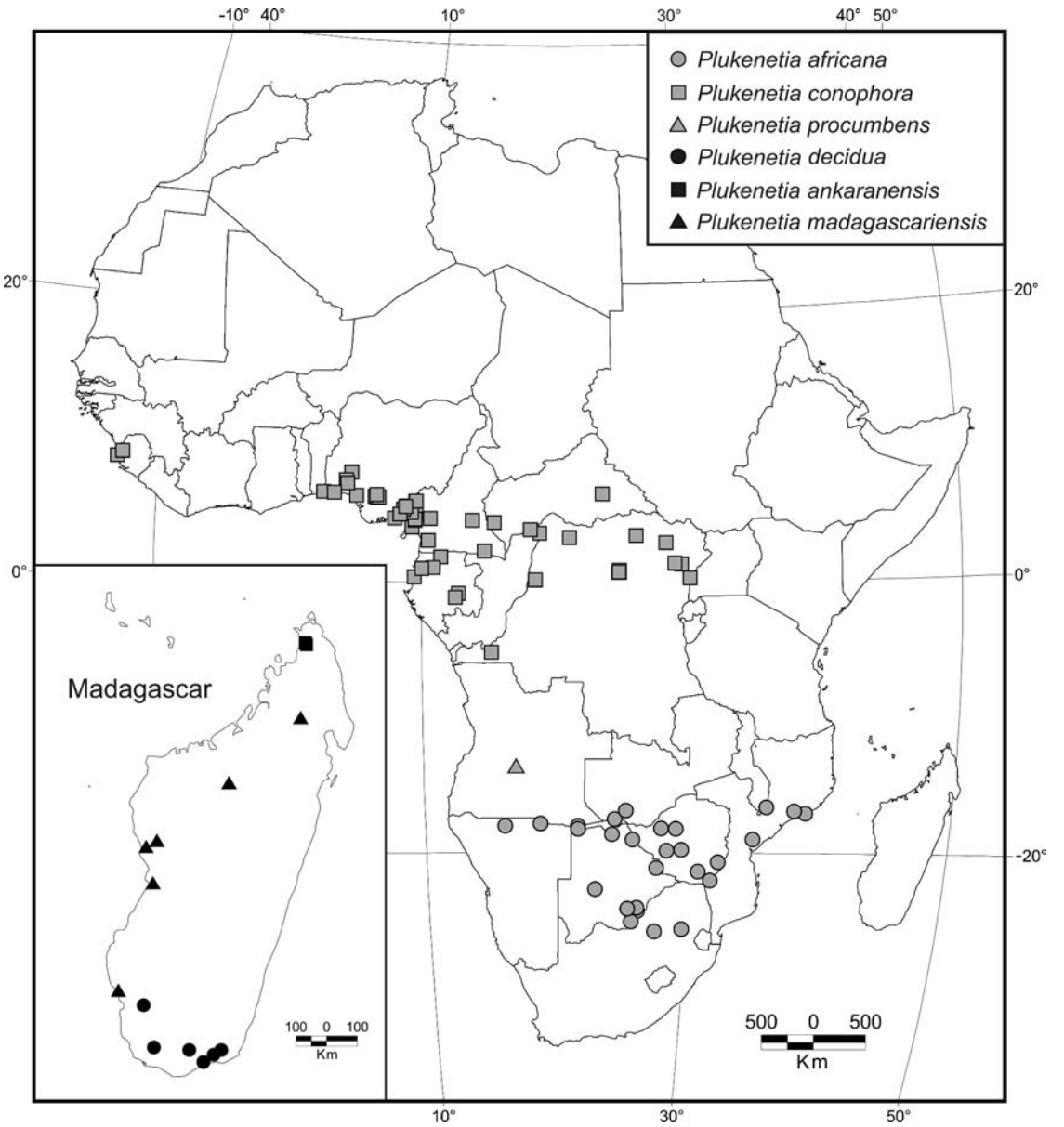

FIG. 5. Distribution of *Plukenetia* in Africa and Madagascar (inset).

sometimes reticulate; stipels and glandular knob absent; basilaminar glandular areas 2–4(–6), irregularly circular to elongate, 0.5–4 mm long, near margin, each area usually comprising many small glands of irregular shape and size; laminar glands absent. **Inflorescence** unisexual or functionally unisexual, axillary, 1(–2) per axil, main axis sparsely puberulous, minor axes moderately to densely puberulous; peduncle 0.2–2.4 cm long; bracts narrowly triangular, very sparsely pubescent, staminate 1–1.2 mm long, pistillate 0.5–1 mm long; staminate inflorescence a narrow thyrse (rarely with one or two branches near base similar to main axis), 4–13 (–20) cm long, cymules condensed to somewhat lax with axes to 4 mm long, sometimes with 1 or 2 apparently nonfunctional pistillate flowers at basal-most nodes; pistillate inflorescence a raceme, 0.5–3 cm long, flowers 1 or 2(3), single per node, axis mostly aborted above [rarely with few staminate flowers in cymule(s)]. **Staminate flower** pedicel 2–7 mm long, slender, glabrous; bud globose, obtuse at apex; sepals 4 or 5, elliptic or narrowly obovoid, 2.2–3.6 × 1.1–1.8 mm, mostly glabrous, acute at

apex; androecium subglobose or ellipsoid, 1.2–2 mm long, comprising 25–40 stamens on small subglobose receptacle, filaments plump-conical, 0.2–0.4 mm long; disc segments numerous, slender-cylindrical, 0.1–0.2 mm long, interstaminal. **Pistillate flower** pedicel 1.5–5 mm long, sparsely or very sparsely puberulous; sepals narrowly triangular, 0.6–1.2 × 0.3–0.7 mm, very sparsely puberulous, often ciliolate; ovary 1.5–3 × 2.5–5 mm (including wings), moderately puberulous, 4 (rarely 5)-winged, wings sparsely puberulous, becoming larger and auriculate in immature fruit stage; styles 4–7.5 mm long, sparsely puberulous, mostly connate into a thick cylindrical column 1–2.5 mm wide, conspicuously dilated to 3–5.5 mm wide at apex, the 4 free style arms 0.5–2 mm long, broad, obscurely bifid, divergent, their inner surface stigmatic; pistillate flowers on staminate inflorescences smaller, with ovary lacking wings, stylar column to 4.5(–7) mm long, not or variously dilated at apex, free style arms absent or < 0.5 mm long. **Fruit** 4 (rarely 5)-lobed, apparently indehiscent, ~2.5–3.5 × 5–7 cm when dry (~5 × 7.5 cm when fresh according to *Osmaston 2599*), glabrous, each carpel subglobose, carinate, keel to 11(–14) mm wide, widest at centre and often appearing wing-like; pericarp 2–3 mm thick when dry. **Seeds** broadly ovoid, ~2.9 × 2.7 × 2.5 cm, surface (tegmen) medium to dark brown, rough, with irregular vertical ridges and reticulations; testa not persistent, pale brown with fine dark brown markings.

Pollen Description. Gillespie (1994), Fig. 19.

Illustration. Pax and Hoffmann (1919), Fig. 5.

Distribution and Ecology. Sierra Leone (not indigenous?), Benin, Nigeria, Cameroun, Equatorial Guinea, Gabon, Congo, and the Democratic Republic of Congo (Zaire) (Fig. 5). A liana of terra firme rainforest, growing in primary, secondary, and degraded forest, gallery forest, and in secondary scrub, cacao and coffee plantations; near sea-level to 750 m; sometimes cultivated. In western Africa (Sierra Leone to Cameroun) flowering collections made in November to March and fruiting collections February to June; in Nigeria seeds are recorded to be available from June to September (Egharevba et al. 2005). In central Africa flowering apparently throughout the year, fruits collected in February and March.

Representative Specimens Examined. SIERRA LEONE. Allen Town, *Deighton 3304* (K); Port Loko, *Deighton 4041* (K), *5018* (K).

BENIN. Cercle de Porto Novo, près la gare de Sahété, *Chevalier 22870* (K, P).

NIGERIA. Benin Prov., Benin Division, Okomu Forest Reserve, *Brenan* & *Onochie 8999* (BM, K, P); Ibadan Prov., Igbajo District, Aba-panu on mile 8 from Ikirun-Igbajo motor road, *Latilo*, *FHI 31764* (K); Calabar Prov., Ikpai District, between miles 68 and 69 on Calabar-Mamfe road, *Latillo*, *FHI 53991* (K); near Modakeke, *Foster 205* (K); Ijebu Prov., Babo Eko, Shasha Forest Reserve, *Ross 87* (BM, MO); Oban District, *Talbot* & *Talbot 1384* (K); Oban District, Oban, *Talbot & Talbot s.n.* (K, MO); Eket District, *Talbot* & *Talbot s.n.* (BM); Aguku District, *N. Thomas 888* (K); Ubuluku, *N. Thomas 2072* (K).

CAMEROUN. **East Prov.:** Bertoua, near catholic mission, *Breteler 816* (K, P). **South-West Prov.:** Kumba District, by the side of River Kindong, N.A. Forest Reserve, Mbalange, Southern Bakundu, *Binuyo & Deramola*, *FHI 35499* (K, P); Victoria, *Maitland 375* (K); Konye, Bakossi Mbambe Forest, Mamfe Road, 4°56′N, 9°30′E, *Nemba* & *Thomas 434* (MO); Kurume, west of Mungo R., 4°55′N, 9°29′E, *D. Thomas 5455* (MO, P), *5456* (MO, P); Banyu, 5°10′N, 9°14′E, *Thomas et al. 5524* (MO); degraded forest at Barombi Kang, Kumba, 4°36′N, 9°27′E, *Thomas & Etuge 6984* (MO); forest around Masaka-Batanga, 5°06′N, 9°10′E, *Thomas & Namata 7790* (MO); forest along Mungo R. by Kurume hammock bridge, 40 km N of Kumba on Mamfe road, *Thomas & Nemba 5419* (MO). **South Prov.:** Bipinde, *Zenker 1583* (BM, L, P); Bipinde, 1900, *Zenker 2234* (A, BM, COI, G, L, MO, O, P, S); Bipinde, 1903, *Zenker 2551* (BM, G, L, MO, P); Bipinde, 1907, *Zenker 3273* (BM, G, K, L, MO, P, S, US), *Zenker 3311* (BM, G, L, P, US), *Zenker 3394* (BM, COI, G, L, P, US); Bipinde, 1912, *Zenker 4451* (BM, G).

CENTRAL AFRICAN REPUBLIC. Région de Yalinga, Haut Oubangui, rive droite au Zaes, *Le Testu 4366* (P); Région de Mbaiki, Station Central de Boukoko, *Tisserant 104* (M, P), *1261* (BM, P), *2045* (BM, P).

EQUATORIAL GUINEA. Sierra del Crystal, *Mann 1739* (syntypes: K, P).

GABON. Environs de Libreville, *Klaine 2284* (K, P); Le Haute Ogooué, Koulamotou, *Le Testu 8183* (BM, P); Oyem, *Le Testu 9194* (P); Ngounie region, Komi, near Sindara, 1°4′S, 10°48′E, *Thomas & Wilks 6418* (MO, P).

CONGO. Lékana, village Ebongo, *Bouquet 2460* (P); Environs de Brazzaville, *Courtet s.n.* (L).

CONGO, DEMOCRATIC REPUBLIC (ZAIRE). **Equateur:** Eala, *Corbisier 1231* (BM, K, MO, P); entre Businga et Banzyville, Territoire Businga, *Lebrun 2013* (MO); entre Libenge et Gemena, Territoire Libenge, *Lebrun 1797* (MO). **Orientale:** Epulu, zone de Mambasa (Ituri), 1°25′N, 28°35′E, *Hart 479* (MO), *780* (MO); Bambesa, Territoire Bambesa, *Gilbert 457* (K); entre Iruma et Mombasa, Territoire Mombasa, *Lebrun 4165* (K); Yangambi, Territoire Isangi, *Léonard 1283* (MO); Malibua, route Yangambi-Ngazi, Territoire Isangi, *Louis 1226* (MO); Yangambi, plateau de la Lusambila, 5 km au N du fleuve, Territoire Isangi, *Louis 3333* (MO); Yangambi, Réserve Flore Isalowe, Territoire Isangi, *Louis 5945* (MO); Yangambi, route Ngazi, Territoire Isangi, *Louis 7980* (MO); Yangambi, Plateau de la Luweo, Territoire Isangi, *Louis 9876* (MO); Yangambi, Territoire Isangi, *Louis 10259* (MO); Yangambi, Plateau de L'Etchwa, Territoire Isangi, *Louis 13218* (K).

Vernacular Names and Uses. Sierra Leone: Awusa (Creole; *Deighton 4041*, *5018*), Owusia (*Elliot 4118*). Nigeria: African walnut (*Lowe 1738*), Akan otoli (*Thomas 1997*), Asala (Yoruba; *Lowe 1738*, *Osseyemeh 3342*), Awusa (Yoruba; *Kennedy 1731*, *Lowe 1738*), Òkp'á (*Thomas 1088*), Omumu (*Thomas 2072*). Cameroun: Casso (Yaoundé; *Hedin 2101*), Casu (*Thomas et al. 5524*), Kaso (Balondo; *Nemba & Thomas 434*). Central African Republic: Kaso (Lissongo; *Tisserant et al. 104*, *1261*, *2045*). Democratic Republic of Congo: Tobe (Lunandi; *Hart 497*, *780*, *1621*, *Omaston 2599*). Gabon (Raponda-Walker

and Sillans 1961): Békasè (Bakèlè), Békasi (Béséki), Bokasu (Bakota), Dugasu (Bapunu), Kasu (fruit, numerous dialects), Mugasa (Éshira, Bavarama, Bavungu), Mukasu (Avili, Banzabi, Baduma), Muti-a-kasu (Baduma), Nsinga-makasu (Loango), Nwisi-wa-kasu (Ngowé), Ogasu (Mpongwè, Galoa, Nkomi, Orungu, Mitaogo, Apindji, Simba, Ivéa, Bavové). Known as African walnut, Nigerian walnut, and Conophor nut, and the extracted oil as Conophor oil in the agricultural and biochemical literature (e.g., Sato et al. 1991; Animashaun et al. 1994; Odoemelam 2003; Egharevba et al. 2005).

Seeds are reported to be edible, and are eaten throughout the species range, in Sierra Leone (*Elliot 4118*), Nigeria (*Thomas 1088*, *Osseyemeh 3342*), Cameroun (*Thomas & Namata 7790*, *Thomas & Nemba 5419*; Hédin 1929), Central African Republic (*Tisserant et al. 104*, *1261*), the Democratic Republic of Congo (*Hart 780*), and Gabon (Raponda-Walker and Sillans 1961). Seeds are reported to be eaten boiled in Cameroun (*Thomas et al. 5524*), cooked in the Democratic Republic of Congo (*Osmaston 2599*), and grilled in Gabon (Raponda-Walker and Sillans 1961), and are sold in markets in Sierra Leone (*Deighton 4041 5018*) and Cameroun (*Hedin 2101*). Ethnomedicinal use includes macerations of leaves and roots for treating asthma and hypertension (Okafor and Okorie in Egharevba et al. 2005). The uncommon 5-lobed fruits are considered to be good luck charms in Cameroun (*Thomas et al. 5524*).

Plants are both cultivated in village farms and encouraged to persist in a semi-wild state on farmland for their edible seeds and for the oil extracted from the seeds (Hédin 1929; Chevalier 1948; Okigbo 1977; Egharevba et al. 2005). The presence of 5-lobed fruits may provide evidence for selection by local farmers (the one seen also lacks the broad keel typically present on each carpel). Recent biochemical research has shown the seeds to have high protein and oil content (Akpuaka and Nwankwor 2000; Akintayo and Bayer 2002; Odoemelam 2003; Oboh and Ekperigin 2004); a similar large-seeded neotropical species, *P. volubilis* L., has attracted interest for its storage protein containing all essential amino acids (Sathe et al. 2002). The species has recently been the focus of agricultural research such as characterizing and improving seed germination and seedling growth (Egharevba et al. 2005; Jiofack and Dondjang 2006a,b).

Discussion. *Plukenetia conophora* is distinct among paleotropical species, and has previously been treated as a separate monotypic genus, either *Angostylidium* (Pax and Hoffmann 1919) or *Tetracarpidium* (Hutchinson and Dalziel 1928, 1958; Pax and Hoffmann 1931). First described under *Plukenetia* (Müller 1864), the species is once again treated in this genus based on many shared characters with neotropical species. The species most closely resembles species of neotropical *P.* sect. *Plukenetia* (species group 1, Gillespie 1993; ''Cylindrophora,'' Pax and Hoffmann 1919), differing only in minor characters such as smaller pollen grains and lack of stipels or glandular knob at the petiole apex, and may indeed belong to this group. The monotypic section *P.* sect. *Angostylidium* is provisionally retained here for this species, pending results of a phylogenetic study.

The species may be distinguished from other paleaotropical species by staminate flowers with a disc and either four and five sepals, large fruits and seeds, and a conspicuous gynoecium with a thick stylar column and four, very short, spreading, dilated arms. In addition, liana habit, axillary inflorescences, a greater number of stamens, and ovoid seeds distinguishes it from *P.* sect. *Hedraiostylus*, and a little expanded staminate receptacle and stamens with filaments from the Madagascan species group. All of these characters distinguishing *P. conophora* in the Palaeotropics are shared with species in the Neotropics (e.g., habit and aspect with *P. polyadenia* Müll.Arg, intrastaminal disc segments with *P. lehmanniana*, gynoecium similar to *P. stipellata*).

The species exhibits two features unusual in *Plukenetia*, irregular and indistinct basilaminar glands and functionally unisexual inflorescences. At the base of the leaf blade on the adaxial surface, the species has two or more glandular areas that are irregular in shape and size and usually composed of many tiny glands. In contrast, other species generally have two distinct, circular or elliptic basilaminar glands.

The species appears to have unisexual or at least functionally unisexual inflorescences, and may be functionally dioecious. The majority of collections examined have staminate or similar apparently bisexual inflorescences, while others have much shorter pistillate inflorescences. The ''bisexual'' inflorescences have one or two pistillate flowers at their base, but these flowers are smaller and morphologically different (e.g., ovary not or only slightly winged, style not or less dilated at apex) from those on pistillate inflorescences, and they appear to be non-functional as no typical mature pistillate flowers or immature fruit have been seen on these ''bisexual'' inflorescences. Pistillate inflorescences may occasionally terminate in a short axis with small staminate buds, but these rarely develop into mature flowers. Only two pistillate collections were seen with staminate flowers

approaching mature size, one with few separate staminate cymules above the pistillate flowers (*Talbot & Talbot 1371*), the second with a single staminate flower in a cymule with a pistillate flower (*Talbot s.n.*).

Unisexual inflorescences and dioecism are unusual in the genus; the majority of species are monoecious with bisexual (and sometimes staminate) inflorescences. Apart from *P. conophora*, the only other species with pistillate and staminate inflorescences is the South American *P. polyadenia*; this latter species appears to be either dioecious or monoecious with unisexual or occasionally bisexual inflorescences (Gillespie 1993). Dioecism and unisexual inflorescences appears, at least in part, to be correlated with habitat and habit; both species are canopy lianas of rainforest with large fruit and similar leaf morphology.

Although the species is, for the most part, morphologically rather uniform across its range, there is some geographical variation in leaf shape. Collections from western Africa (including all collections from Sierra Leone and Benin) generally have ovate leaf blades, rounded to shallowly cordate bases, and triplinerved to weakly palmate venation, while those from central Africa most often have elliptic blades, obtuse to rounded bases, and triplinerved venation.

The small population in Sierra Leone is highly disjunct from the main range of the species from Benin to central Africa. The species is likely not indigenous in Sierra Leone, but appears to have been introduced for its edible seeds. Two of four collections indicate cultivation, and Deighton (*5018*) comments that it is apparently not indigenous in Sierra Leone. The population is also not morphologically distinct from other west African collections.

Both syntype collections have staminate inflorescences with small, apparently sterile pistillate flowers. The collection having the most duplicates, *Mann 2202*, is selected as lectotype. Two of the three duplicates appear to have been annotated as *Plukenetia conophora* by Müller; the one annotated as ''originalis'' is selected as lectotype.

PLUKENETIA sect. HEDRAIOSTYLUS (Hassk.) Müll.Arg., D.C. Prodr. 15 (2): 772. 1866. *Hedraiostylus* Hassk., Tijdschr. Natuurl. Gesch. Physiol. 10: 141. 1842.—TYPE: *Hedraiostylus glaberrimus* Hassk., nom. illeg. [= *Plukenetia corniculata* Sm.].

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

This species group, previously most commonly treated as the genus *Pterococcus* (e.g., Govaerts et al. 2000), is treated here as *Plukenetia* sect. *Hedraiostylus*, which takes precedence over *P.* sect. *Pterococcus*. This paleotropical section comprises two African species, *P. africana* and *P. procumbens*, and one Asian species, *P. corniculata*. Most recent floras considered these species as members of *Pterococcus* (Hutchinson and Dalziel 1958; Backer and Bakhuizen van den Brink 1963; Airy-Shaw 1971, 1975, 1981, 1982, 1983; Whitmore 1973; Dyer 1975; Grierson and Long 1987; Radcliffe-Smith 1996); few treat the species under *Plukenetia* (Phillips 1951; Leistner 2000; Germishuizen and Meyer 2003). The species of this section may be distinguished from other paleotropical species by very short styles that are shorter than or equal in length to the ovary, small capsules, and small lenticular seeds. In addition, they may be distinguished from *P.* sect. *Angostylidium* by their terminal, leaf-opposed inflorescences, fewer stamens, absence of a staminate disc, and from the Madagascan species group by their stamens with filaments and little expanded staminate receptacles.

The three species of *P.* sect. *Hedraiostylus* may be most easily distinguished from each other on the basis of foliar characters such as leaf blade size and shape, petiole length, basilaminar gland presence, size, and number, and stipel presence. Style morphology (including shape and degree of connation) and fruit morphology (particularly the size and shape of the appendage on each carpel lobe) provide additional distinguishing characters.

2. PLUKENETIA AFRICANA Sond., Linnaea 23: 110. 1858. *Pterococcus africanus* (Sond.) Pax & K. Hoffm., Pflanzenr. IV.147.IX.(Heft 68): 22. 1919.—TYPE: South Africa. Megalisberg, Oct., *Zeyher 1522* (holotype: S!; isotypes: BM!, G!, K!).

Plukenetia hastata Müll.Arg., Flora 47: 469. 1864.—TYPE: Mozambique. ''Zambesica, on the Lower Zambezi,'' *Kirk s.n.* (holotype: K!).

Pseudotragia schinzii Pax, Bull. Herb. Boissier, ser. 2. 8: 635. 1908.—TYPE: Namibia. ''Amboland, Otjiheveta,'' *Schinz 895* (holotype: G, not seen; isotype: K!).

Pseudotragia scandens Pax, Bull. Herb. Boissier, ser. 2. 8: 636. 1908.—TYPE: Namibia. ''Amboland, Oohama,'' Mar 1886, *Schinz 894* (holotype: G, not seen; isotype: K!).

Monoecious vine or sometimes perennial herb with thick woody rootstock; stems twining, scan-

dent or sometimes trailing on ground, slender, sparsely to moderately pubescent; new shoots from rootstock initially erect. Stipules linear-lanceolate or linear-triangular, ca. 1 mm long. **Leaves** with petioles 0.2–0.9 cm long, sparsely to densely pubescent; blades narrowly triangular, lanceolate, or linear-lanceolate, 3–8 × (0.15–)0.3–1.5(–3) cm, often with hastate basal lobes and then to 3(–4.5) cm wide, thin to thick-chartaceous, glabrescent to sparsely pubescent with major veins usually sparsely or moderately pubescent, narrowly acute or rarely broadly acute at apex, hastate, truncate, shallowly cordate, rarely sagittate or obtuse at base, basal lobes when present usually triangular, to 1(–1.5) cm long, pointed or rounded, and oriented horizontally (rarely directed downwards and then base sagittate), margins remotely serrulate to serrate, especially along basal half; venation weakly palmate or 3-nerved at base, secondary veins brochidodromous, 2–8 on each side of midrib, tertiary veins weakly percurrent or reticulate; stipels usually present, 2, 0.1–0.6 mm long; basilaminar glands 2(–4), circular or elliptic, 0.2–0.3 (–0.4) mm in diam, marginal, often obsure or sometimes absent; laminar glands absent or rarely 1–2(–8), minute. **Inflorescence** a narrow thyrse, 1–7(–10) cm long, bisexual, terminal but appearing leaf-opposed, or rarely terminal on short shoots; axis sparsely to moderately pubescent basally to glabrescent distally; peduncle 1–8 mm long; pistillate flower 1 at basal-most node, staminate flowers numerous above in small, very condensed cymules; bracts narrowly elliptic or lanceolate, 1.5–3 mm long, glabrous. **Staminate flower** pedicel 1–1.7 mm long, glabrous to very sparsely pubescent, especially near base; bud globose, broadly obtuse to rounded at apex; sepals 4, ovate or elliptic, 1.1–1.5 × 0.6–1 mm, glabrescent, acute at apex with thickened tip; androecium subglobose, ~1 mm in diam, comprising 15–20 stamens densely packed on small convex to subglobose receptacle; filaments conical, 0.2–0.4 mm long; disc absent. **Pistillate flower** pedicel 3–10(–14) mm long, very sparsely to moderately pubescent; sepals ovate or elliptic, 2–3 × 0.8–1.5 mm, glabrescent to sparsely pubescent; ovary 1–2 × 1.5–3 mm (excluding wings), hirsute, 4-winged, wings 0.8–1.5 mm long, rounded, sparsely hirsute; styles 1–1.4 mm long, mostly connate into a stout hirsute column 0.7–1 mm long, the 4 prominent stigmas forming a cross 1.2–2.2 mm across at apex, each stigma obtusely obtriangular, glabrous. **Fruit** a 4-lobed capsule, 6–8 × 11–17 mm, sparsely pubescent, surface irregularly angular-verrucose, each carpel lobe with wing 1–3 mm long; pedicel 0.6–1.5(–2.5) cm long. **Seeds** broadly lenticular, 6.5–8 × 5.5–7.5 × 2.5–4 mm (including keel), obtuse-triangular in outline, laterally compressed, with radial keel 0.5–1.2 mm wide, surface coarsely and irregularly reticulate, pale brown or pale greenish-brown, often with darker orange-brown markings; testa persistent.

Pollen Description. Gillespie (1994), Fig. 18.

Illustrations. Pax and Hoffmann (1919), Fig. 7; Radcliffe-Smith (1996), Tab. 44.

Distribution and Ecology. Zambia, Mozambique, Zimbabwe, Botswana, Namibia, and South Africa (Fig. 5). A vine or perennial herb with twining or trailing stems growing in open or wooded savanna, woodland, or open forest, on sand or sandy soil; mostly 900–1200 m, 100–500 m in Mozambique and SE Zimbabwe. Flowering and fruiting collections made between September and April.

Representative Specimens Examined. ZAMBIA. Machili District, Machili, *Fanshawe 5957* (K).

MOZAMBIQUE. entre Mocubela e Bajone, a 15.5 km de Mocubela, *Grandvaux Barbosa & Carvalho 4267* (K); Lugela District, Moëbede road, *Faulkner 299* (K); Marica/E Sofala District, ~10 km N of Mwanza where the road crosses the railway line, between Dondo and Inhaminga, *Pope & Müller 517* (K); Gaza Dist., Border Post, Malvernia, *Thompson 2* (K, MO).

ZIMBABWE. Shangani/Bubi District, Gwampa Forest Reserve, *Goldsmith 65/56* (K, MO); Chipinga District, E side of Sabi R. at Dotts Drift, *Goodier 661* (K); Nyamandhovu District, Pasture research station, *Plowes 1928* (K); Wankie District, main camp along Dopi Pan road, *Rushworth 1308* (K); Wankie District, Game Reserve, Ngwashla Rd., *Wild 4759* (COIMB, K, S).

BOTSWANA. Kweneng District, 15 mi from turn off towards Ngware, *Hansen 3251* (K); Mochudi, *Harbour 6333* (BM); North District, Chobe Game Scout Camp on Savuti R., *Pope et al. 834* (K); Francistown, *Rand 5* (BM); 162 km N of Nata on road to Kasane, *Vahrmeijer Stee 3164* (K); Northern Division, Khardoum Valley, 1.5 km E of SW Africa border, *Wild & Drummond 7049* (K).

NAMIBIA. Dikundu, *Gless 11378* (K); c. 10 mi from Katima on road (Finaughty's) to Singalamwe, *Killick & Leistner 3188* (K); 3 mi S of Omuramba Mpungu on rd. to Tsinsabis, 17°50′S, 18°40′E, *Winter 3908* (K); Ndonga Camp at junction of Omuramba Omatako and Okavango River, *Winter & Marais 4618* (K).

SOUTH AFRICA. ''South African Gold-fields,'' 1840, *Baines s.n.* (K); Zoutpansberg, E of Pan, *Schweickerdt & Verdoom 552* (K).

Vernacular Name. Mozambique: Nama-han-ham (Quelimane; *Grandvaux Barbosa 4267*).

Discussion. This species may be easily distinguished by its narrow leaves, which often have a distinctly hastate base. Basilaminar glands are typically very small and sometimes absent, in contrast to the more conspicuous glands of other species. A pair of very small stipels or glandular knobs is usually present at the petiole apex. The species has a short wing on each carpel lobe and short styles that are mostly connate and obsurely 4-lobed at the apex, both states intermediate between those found in the other two species of the section, *P. corniculata* and *P. procumbens*.

The species shows considerable variation in leaf blade shape and degree of development of the hastate base. Leaf blades typically vary from linear to lanceolate or narrowly triangular, with a non-hastate or obscurely to prominently hastate base, and a remotely serrulate to distinctly serrate margin. Although there is some variation within a collection, such as short- versus long-hastate or hastate versus non-hastate base, most variation appears to be among collections and some appears to be geographically based. In Botswana, Zambia, and Zimbabwe leaf blades are mostly very narrow and linear, narrowly lanceolate, or very narrowly triangular in shape, while in South Africa and Namibia blades tend to be narrowly triangular. Leaf variation is most extreme in Mozambique where collections may have relatively broad leaf blades (e.g., *Pope and Muller 517*), very large hastate lobes, scattered laminar glands on the abaxial surface, large and sometimes up to 4 basilaminar glands, and in one collection (*Pope and Muller 517*) numerous basilaminar glands. Basal leaf lobes may occasionally be oriented downwards rather than horizontally, and thus appear sagittate (e.g., *Pope 458*).

Some of the leaf variation both within and between collections may be attributable to age and position on the plant. Stems appear to be intially erect or sprawling from a perennial rootstock, becoming long and twining. There appears to be some tendancy for leaves near the plant base to be broader, and those on long twining shoots to be narrower. Basal-most leaves often lack a hastate base (e.g., *Pope and Muller 517*, with elliptic obtuse-based basal leaves, and *Schinz 895*).

The species *P. hastata* was described by Müller (1864) and distinguished primarily based on a scandent habit from *P. africana*, then thought to have an erect habit. Prain (1913, 1925) following Müller continued to recognize *P. hastata*, based on scandent stems, finely dentate leaves, sometimes deeply sagittate at the base, and eight stamens, as distinct from *P. africana*, considered at the time to be an erect plant with coarsely toothed leaves that are never sagittate at their base and 12 stamens. Pax (1919), correctly recognizing that these differences do not hold, treated *P. hastata* as a synonym of *P. africana* and the species as having twining stems and typically hastate leaf blades. In addition, examination of staminate flowers in the present study revealed a stamen number (15–20) greater than that recorded for either species.

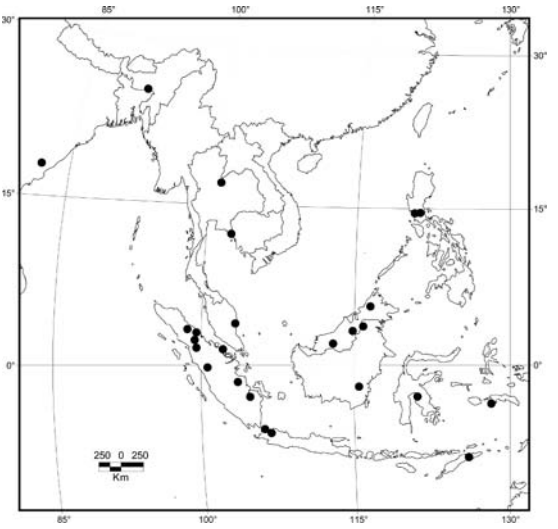

FIG. 6. Distribution of *Plukenetia corniculata*.

3. PLUKENETIA CORNICULATA Sm., Nova Acta Regiae Soc. Sci. Upsal. 6: 4. 1799. *Hedraiostylus corniculatus* (Sm.) Hassk., Cat. Hort. Bogor Alt. 234. 1844. *Sajorum corniculatum* (Sm.) Dietr., Synops. Pl. 5: 331. 1852. *Pterococcus corniculatus* (Sm.) Pax & K. Hoffm., Pflanzenr, IV.147.IX.(-Heft 68): 22. 1919.—TYPE: Indonesia, Moluccas, Ambon Island, ''Bagulae Regione, Amboinae'', *Rumphius* (specimen presumably lost, illustration Tab. 79, Fig. 2. in Rumphius, Herb. amboin. 1. 1741, between pages 193 and 194). Fig. 1.

Monoecious vine or slender liana; stems twining, sparsely to moderately pubescent, becoming woody. Stipules narrowly triangular or lanceolate, 1.2–2(–2.8) mm long. **Leaves** evergreen; petioles [1-; square brackets refer to collections from Timor] 2–8(–13) cm long, moderately or sparsely pubescent; blades ovate, triangular-ovate, oblong-ovate, or elliptic [4–] 7–16 × [2–] 4–11 cm wide, thin-chartaceous, very sparsely pubescent or glabrescent with major veins usually sparsely or moderately pubescent above, acute-caudate at apex with tip 0.6–2.3 cm long, cordate at base with U-shaped sinus [0.1–] 0.5–2.3 cm long, margins finely serrate or rarely serrate; venation palmate, secondary veins semicraspedodromous, 2–3(4) [–5] on each side of midrib, tertiary veins percurrent or sometimes reticulate; stipels 2, ~0.5–1 mm long, usually strongly curled adaxially; basilaminar glands 2, circular or elliptic, [0.3–] 0.5–1 mm in diam, marginal; laminar glands absent. **Inflorescence** a narrow raceme, 1.5–5 cm long, bisexual, terminal but appearing leaf-opposed, sometimes terminal on short shoots, or rarely axillary (some Thailand collections), axes puberulous; peduncle

1–8 mm long; flowers 1 (rarely 2) per node, pistillate flower 1 at basal-most node, staminate flowers numerous above; bracts narrowly triangular, ~1 mm long. **Staminate flower** pedicel 1.3–2.5 mm long, glabrescent; bud globose, obtuse at apex; sepals 4, elliptic or ovate, 0.7–1.1 × 0.5–0.8 mm, sparsely pubescent near base, acute at apex; androecium globose, 0.4–0.6 × 0.6–0.8 mm, comprising 8–14 stamens on small globose or convex receptacle; filaments conical, < 0.1 mm long; disc absent. **Pistillate flower** pedicel 1.5–9 mm long, sparsely puberulous to glabrescent; sepals narrowly triangular or lanceolate, 1.2–2.2 × 0.5–1 mm, glabrescent; ovary 1–2.5 mm in diam (excluding wings), sparsely or very sparsely puberulous with puberulent medial line on each carpel extending along wing margin, 4-winged, wings 0.5–2 mm long, elongating to 13 mm and becoming glabrescent in immature fruit stage; styles completely connate into a small depressed-globose column, 0.5–0.7 × 0.8–1.1 mm, glabrous, with cross-shaped stigmatic surface at apex. **Fruit** a 4-lobed capsule, [5–] 7–11 × 15–20 mm, glabrescent, surface irregularly verrucate, each carpel lobe with central strap-shaped wing 6–12 × 2–3 mm; pedicel [0.6–] 2–5 cm long. **Seeds** broadly lenticular, 8–11 × 6.5–8 × 5–6.5 mm, obtuse-triangular in outline, laterally compressed, with radial keel 0.3–0.7 mm wide, surface smooth, cream, pale orange-brown, or pale to medium brown with dark orange or dark brown irregular markings; testa persistent.

Pollen Description. Gillespie (1994).

Illustration. Narasimhan et al. (1989), Fig. 1.

Distribution and Ecology. Widespread but uncommon throughout SE Asia and Malesia, in NE (Assam) and SE (Andhra Pradesh) India (Narasimhan et al. 1989), Burma (?), Thailand, Philippines, Malaysia, and Indonesia (Fig. 6). Also recorded, but not confirmed, from Sikkim in NE India (Grierson & Long 1987) and Bangladesh (*Huq 10780*, specimen recorded but not found at L). A slender twining liana found in clearings and other disturbed areas of lowland wet (evergreen) and moist (deciduous) forest; 50–550 m; sometimes cultivated. Flowering collections were made in June in Bangladesh, August in India, December in the Philippines, July and August on Borneo, and throughout the year on Java and Sumatra. Fruiting collections were made in August in India, July and September in Thailand, June on the Malay Peninsula, December in the Philippines, June and August in Sarawak, October in Sulawesi, and April to August in Java and Sumatra. Reported to be the larval foodplant of the Nymphalid butterfly, *Ariadne isaeus*, in Malaysia (*Kirton T.22*).

Representative Specimens Examined. INDIA. **Assam:** Cherrapunjee, Khasi Hills, *Koelz 31112A* (L); ''Upper Assam,'' *Jenkins 517* (K).

THAILAND. **Northern:** Phitsanulok, Tung Salaeng Luang, *Larsen 552* (L). **Southeastern:** Chanthaburi, Klawng Kloi, *Kerr 9241* (BM, K, L).

PHILIPPINES. **Luzon**. Bataan Prov., Ayam River, Lamao, *Edaño*, *PNH 4157* (A, L); Rizal Prov., *Ramos*, *Bur. Sci. 24086* (BM, BO, K, L, MO, NY, US).

MALAYSIA. **Pahang/Trengganu:** Kuantan District, Bukit Galing Forest Reserve, *Kirton T.22* (K). **Sabah:** Tamkunan District, Gn. Trusmadi, *Mantor SAN 125574* (KEP, SAN). **Sarawak:** Baram (4th Division), house compound of Long Selstong Ulu, cultivated, *Chin 2712* (A, L); Kapit, upper Rejang River, *Clemens & Clemens 21257* (BO, K, MO, NY); without precise locality, *Smythies 14073* (K-2).

INDONESIA. **Java:** Batavia, Depok, *Bakhuizen van den Brink 5490* (BO, G, K, L), *5771* (BO, K, L); Goenoengkantjana, Distr. Lobakkidoel, res. Bantam, *Koorders 40372b* (BO, L), *Koorders 41507b* (BO, L), *Koorders 41509b* (BO, L), *Koorders 41720B* (BO, K, L, UC); without precise locality, *Zollinger 3167* (BM, G, G-DC). **Kalimantan:** Hayup, *Winkler 2295* (L); Kwaru, Suwaring, *Winkler 3096* (L). **Sulawesi:** Lelewao District, Preho, *Kjellberg 2544* (S). **Sumatra:** Sumatera Selatan, Komering Oeloe, *Grashoff 587* (BO, L); Sumatera Utara, Middle Habinsaran near Parsoboeran, *Lörzing 7821* (L); Sumatera Barat, Kampong Sabalading on slope of Gunong Sago near Pajakumbuh, cultivated, *Meijer 7309* (K, L); Soengai Lesing, *Posthumus 994* (BO, L); vicinity of Loemban Ria, Asahan (east coast), *Rahmat Si Boeea 7593* (A), *7827* (A); Si Mandi Angih, on the Soengei Kanan, Subdiv. Laboehan Batoe, District Kota Pinang, *Rahmat Si Toroes 3948* (NY). **Timor:** precise locality and collector unknown (L-0023061, L-0023062, L-0023063, L-0023064, L-0023065, L-0023066, L-0023067).

Vernacular Names and Uses. India. Andhra Pradesh: Kodigandlam (Narasimhan et al. 1989). Malaysia. Sarawak: Buah andu (Iban; *Smythies 14073*), Buah palidung (Kelabit; *Christensen & Apu 318*), Lãot (Kenyah; *Chin See Chung 2712*). Indonesia. Sumatra: Gandi riman (*Posthumus 994*), Paina paina (*Grashoff 587*), Pepina (*Bequin 407*), Pina-pina makanan (*Rahmat Si Toroes 3948*); Java: Aroj tangtang anging (*Koorders 40372b*, *41509b*); Flores: Lanteng wasé (*Schmutz 4178*); Sunda region: Aroy tangtang angien (Hasskarl 1842).

The species is recorded as cultivated in Sarawak (*Chin See Chung 2712*, *Christensen & Apu 318*, *Smythies 14073*) and Sumatra (*Meijer 7309*). In Sarawak young shoots, leaves, and young fruits are recorded to be eaten as a vegetable, while the mature seeds are eaten as nuts and are said to taste similar to peanuts (*Chin See Chung 2712*, *Christensen & Apu 318*). It is reported to be cultivated as a vegetable by Dayaks and the distinctive form of the fruit is sometimes seen tatooed, 5 or 6 in a vertical row, on the back of an Iban (*Smythies 14073*). In India a paste made from young leaves is used as an oral laxative medication (Narasimhan et al. 1989). In Australia the species was collected under cultivation in a garden, where it was called Borneo pea (*Waterhuse 5980*).

Discussion. The species may be easily distin-

guished from other members of *P.* sect. *Hedraiostylus* by its prominently 4-winged capsule (Figs. 1I, J) and larger leaf blades with a distinctly cordate base (Fig. 1A). Leaves are also distinct in their long petioles (2–8 cm long), caudate apex, and prominent basilaminar glands and stipels. Styles are completely connate, and both stylar column and filaments are shorter than in the other two species. This is the only species of *Plukenetia* known from Asia.

Plukenetia corniculata was the second species of *Plukenetia*, after the neotropical *P. volubilis*, to be illustrated (Rumphius 1741, as ''Sajor volubilis'') and formally described (Small 1799). However, for much of its history, the species has been known under a variety of other names. Hasskarl (1842) based his new genus *Pterococcus* on this species, but renamed the species ''Pterococcus glaberrimus,'' an illegitimate name being based on *P. corniculata*. Soon after, Hasskarl (1843) created a second genus, *Hedraiostylus*, and transferred the species, naming it ''Hedraiostylus glaberrimus,'' again an illegitimate name. Later legitimate combinations include *Hedraiostylus corniculatus*, *Sajorum corniculatum*, and *Pterococcus corniculatus*, the last used by Pax and Hoffmann (1919) and by most subsequent authors.

The species is most densely distributed on the island of Sumatra and less so on Borneo. Distribution outside this area appears to be scattered and sparse. The reason may be that it is rarely collected due to its naturally sparse distribution in these peripheral areas and its vine habit. An alternative explanation may be that it was introduced and cultivated and/or naturalized in at least some of these areas for its edible seed. Many of the collections from these areas are old and some are recorded as cultivated. All collections seen from Timor (pre-1829 based on determinations by A. Zippelius), Java (numerous collections, all pre-1923, and all but one likely cultivated), Sulawesi (one collection, 1929), and the Moluccas (type collecton only, pre 1800) are old, as are most from Assam, India (all but one pre-1890 or undated). The record from Burma could not be verified, since contradictory locality information is given on the only collection seen, *Griffith 4716* (Mergui [Burma] on one sheet, Malakka [Malaysia] on two sheets at K; undated). Four of five collections from Sarawak were recorded as cultivated or from gardens or house compounds.

4. PLUKENETIA PROCUMBENS Prain, Bull. Misc. Inform. Kew 1912: 240. 1912. *Pterococcus procumbens* (Prain) Pax & K. Hoffm., Pflanzenr. IV.147.IX.(Heft 68): 23. 1919.—TYPE: Angola, Benguella, Ganguella, on the Cubango River at Princeza Amelia, 1520 m, 27 Jan 1907, *Gossweiler 2540* (holotype: BM!, fragment at K!; isotype: COI!).

Monoecious perennial herb, with woody rootstock; stems procumbent, sprawling, pubescent. Stipules small. **Leaves** with petioles 0.2–0.5 cm long, moderately pubescent; blades elliptic or ovate, 2–4.5 × 1.3–3.3 cm, chartaceous, sparsely pubescent below, glabrous or very sparsely pubescent above with major veins sparsely pubescent, drying grey-green with purplish tinge, obtuse to short acuminate at apex, rounded to broadly obtuse at base, margin finely serrate; venation 3-nerved at base, secondary veins brochidodromous, 2–5 on each side of midrib, tertiary veins weakly percurrent or reticulate; stipels absent; basilaminar glands 2–12(–20), somewhat irregular in size and shape, usually circular or elliptic, 0.2–0.8 mm long, often dark purple, usually in an irregular line near margin; laminar glands absent. **Inflorescence** a narrow raceme, 3–8 cm long, bisexual, terminal but usually appearing leaf-opposed, axis moderately pubescent; peduncle 2–5 cm long; flowers 1/node, pistillate flower 1 at basal-most node, staminate flowers numerous above on axis 1–4 cm long; bracts lanceolate, 2–3 mm long, glabrous or very sparsely pubescent. **Staminate flower** pedicel 2.5–3.5 mm long, pubescent; bud globose, broadly obtuse to rounded at apex; sepals 4, ovate, ~2 × 1 mm, acute at apex; androecium ~1 mm in diam, comprising ~12 stamens densely packed on small convex to globose receptacle; filaments slender, dilated at base, ~0.4 mm long; disc absent. **Pistillate flower** pedicel 3–10 mm long, pubescent; sepals ovate or lanceolate, 2.5–4 × 1–2 mm, sparsely pubescent medially; ovary 1–2 × 1.5–2.5 mm (excluding wings), densely pubescent, 4-winged, wings to 1 mm long, sparsely to moderately pubescent; styles 1.2–1.8 mm long, glabrous, partly connate into a column ~1 mm long, 0.5–0.6 mm wide at base, the 4 style arms divergent, ~2 mm across at apex, each arm dilated and recurved with the adaxial surface entirely stigmatic. **Fruit** a 4-lobed capsule, ~6 × 12–20 mm, sparsely pubescent, surface densely papillose, each carpel lobe with central tubercle ~1 mm long; pedicel ~11–13 mm long. **Seeds** not seen.

Distribution and Ecology. Angola, known only from the type collection (Fig. 5). A perennial, woody-based, mostly herbaceous plant with decumbent stems, collected on clayey soils in short thickets in the interior highlands, ~1500m. The

single collection with flowers and immature fruit was collected in January.

Discussion. This species may be distinguished by its small elliptic leaf blades with a rounded or broadly obtuse base. Leaves are mostly purplish tinged, with small, often numerous basilaminar glands, and lack stipels. Compared with the other two species of *P.* sect. *Hedraiostylus*, the styles are longer and only partly connate, the inflorescences have longer peduncles (2–5 cm versus <1 cm) that are longer than the flower-bearing part of the axis, and each capsule lobe bears a rounded tubercle, much shorter than the wing of the other two species.

The species was described as a perennial herb with a woody base and has numerous highly branched radiating prostrate stems. If indeed the species has a non-scandent habit, this would be different from the twining vine or liana habit of all other species of the genus. While stems may be sprawling, there is no evidence that they are twining on the single collection known. The closest species in habit, and also likely the most closely related, is *P. africana*, which has a perennial woody rootstock and stems that appear to be initially erect or sprawling, becoming long and twining.

Prain (1912) distinguished his new species based on prostrate habit, leaf blades with broadly rounded base, and short petioles. He later also used inflorescence position, terminal versus lateral racemes, to distinguish the species from *P. africana* (Prain 1913). However, neither inflorescence position nor petiole length can be used to distinguish the two species. Inflorescences of both species are terminal and may become leaf-opposed, although inflorescences of *P. africana* are more typically and prominently leaf opposed, while those of *P. procumbens* appear to become so only at a later stage and not prominently so. This difference is likely due to a difference in habit, few long twining sympodial stems each with numerous inflorescences in *P. africana* versus numerous shorter highly branched stems each with few inflorescences in *P. procumbens*. Pax and Hoffmann (1919) used habit as the main character to distinguish the two species.

Information on the locality of the type collection is somewhat contradictory, though appears to refer to the same location. The BM specimen gives the locality as ''praesidium of the Princeza Amelia, Cubango,'' the K specimen as ''praesidium of the Princeza Amelia – Cubango, Ganguellas,'' the COI specimen as ''Vila da Ponte, Ganguelas, Huila,'' while the type description gives ''Benguella; Ganguella, on the Cubango River at Princeza Amelia, 1520 m.''

Madagascan Species Group

The three Madagascan species form a distinct group that has yet to be assigned to a section; the single species known up to now has always been included within *Plukenetia*. Unique among paleotropical species, they share an androecium of sessile anthers on a prominent elongate receptacle. In addition, the group differs from *P.* sect. *Hedraiostylus* in their prominent styles (3.5–16 mm long) longer than the ovary, distinctly carinate fruit, and broadly ellipsoid to subglobose seeds, and from *P.* sect. *Angostylidium* in the absence of a staminate disc. Their medium-sized fruit (2–4 cm wide) and seeds (both unknown for *P. madagascariensis*) are intermediate in size between the small capsules of *P.* sect. *Hedraiostylus* and large fruit of *P. conophora*. All three species have two conspicuous basilaminar glands on the leaf blade adaxial surface, as typical of most *Plukenetia* species.

Characters variable within the Madagascan species group include style connation, shape and length, androecium shape and size, anther number, inflorescence type, length, and position, leaf blade shape, and presence of glandular knobs at the petiole/blade junction.

5. **Plukenetia ankaranensis** L.J. Gillespie, sp. nov.—TYPE: Madagascar, Prov. Antsiranana, Special Reserve #3, Ankarana, ~7 km SE of Matsaborimanga, trail between Camp Anglais and river, ~3 km SW of Camp Anglais, 12°55′S, 49°06′E, ~150 m, 28 Nov 1990, *Gillespie 4076* (holotype: MO!; isotypes: CAN!, DAV!, G!, K!, L!, NY!, P!, TAN!, US!; FAA preserved material at MO). Figs. 2, 3A–D.

Plukenetia madagascariensis Leandri et *P. decidua* L.J. Gillespie affinis, a quibus differt stylis brevioribus connatis omnino columna obovata.

Monoecious liana; base often expanded and bulbous; stems glabrous or sparsely pubescent distally, sometimes glaucous; older branches becoming thick, woody, and often twining. Stipules triangular, ~0.5 mm long. **Leaves** with petioles (0.8–)1.5–6 cm long, moderately to densely puberulous; blades ovate, oblong-ovate, or suborbicular, (3–)5–10 × (2–)4–6 cm, chartaceous, glabrescent to sparsely puberulous with major veins puberulous, acuminate at apex with tip 3–12 mm long, truncate to shallowly cordate at base with sinus to 9 mm deep, margins crenate-serrate; venation 3-nerved at base or weakly palmate, secondary veins semicraspedodromous or sometimes craspedodromous, 2–4 on each side of midrib, tertiary veins percurrent or sometimes reticulate; stipels and glandular knob absent; basilaminar glands 2, circular, (0.2–)0.4–

0.8 mm in diam, marginal; laminar glands absent. **Inflorescence** a racemose thryse, (2–)5–16 cm long, bisexual or sometimes staminate, terminal but becoming leaf-opposed, axes puberulous to glabrescent; peduncle usually absent (and then pistillate flower basal) or sometimes up to 0.2 cm long; pistillate flowers (0)1–2(–3), 1 per node at basal-most node(s) (rarely in basal bisexual cymule or emerging from stem below inflorescence), staminate flowers numerous above in cymules; cymules lax to moderately condensed, primary cyme axes (1.5–)5–12(–22) mm long, the longest ones rarely subtended by a reduced leaf, secondary axes to 3 mm long; bracts linear-lanceolate, linear-triangular, or lanceolate, sparsely puberulent, staminate 1.5–3 mm long, pistillate 1.5–7 mm long. **Staminate flower** pedicel 5–11 mm long, sparsely puberulous; bud ovoid, bluntly acute at apex; sepals 4, narrowly elliptic or lanceolate, 1.2–2.2 × 0.4–1 mm, glabrous or sparsely puberulous, whitish or pale yellowish green, acute and thickened at apex, reflexed at anthesis; androecium oblong-cylindrical, 0.6–1 × 0.5–0.8 mm, comprising 15–20 sessile yellow anthers densely packed on a stalked, cylindrical receptacle. **Pistillate flower** pedicel 2–12 mm long, sparsely puberulous; sepals narrowly lanceolate, 1.5–2.4 × 0.4–0.5 mm, green, glabrescent; ovary 1–2.5 × 1.5–5.3 mm, 4-horned, horns 0.5–2 mm long; styles completely connate into an obovoid or obconical column, 3.5–5.5 mm long, 0.6–1 mm wide at base, dilated to 1.8–2.5 mm at apex, green, often somewhat 4-lobed distally; stigmas forming a raised circular, often somewhat lobed disc at apex. **Fruit** a 4-lobed capsule, ~1.6 × 3–4 cm, green, surface verrucose and minutely papillose with papillae bearing minute hairs, each carpel lobe carinate, keel widened centrally into horn-like wing 0.8–1 cm long; pedicel 0.9–1.3 cm long. **Seeds** subglobose, 1.5–1.8 × 1.6–1.7 × 1.4–1.7 cm, ventral surface distinctly angular, dorsal surface rounded, surface (tegmen) smooth to somewhat verrucate, pale brown; testa whitish, not or partly persistent.

Pollen. Tricolpate, suboblate (P/E = 0.71–0.80), polar axis 28–33 μm, equatorial axis 35–45 μm; amb subcircular; angulaperturate, colpus broad with margins uneven and jagged, exine 1.5–2 μm thick, evenly thickened or slighter thinner towards margin, tectum foveolate (vouchers: *Gillespie 4074*, *4076*).

Distribution and Ecology. Known only from the Ankarana Massif in northern Madagascar (Fig. 5), where it grows in openings within dry forest on eroded limestone pavement, 100–200 m. A liana with branches that twine on shrubs or small trees or sprawl over bare rock pavement (Figs. 3A, C). Flowering and fruiting specimens collected in late November and early December.

Specimens Examined. MADAGASCAR. **Antsiranana:** Special Reserve #3, Ankarana, ~7 km SE of Matsaborimanga, trail between Camp Anglais and river, ~3 km SW of Camp Anglais, 12°55′S, 49°06′E, *Gillespie 4074* (CAN, K, MO, P, TAN, US), *Gillespie 4075* (CAN, MO), *Gillespie 4088* (CAN, K, MO, TAN); Réserve Speciale Ankarana, Lac Vert, ~7 km SE of Matsaborimanga, 12°55′S, 49°06′E, *Lees s.n.* (CAN, US); southwest of Antsiranana, Réserve Speciale de Ankarana, 12°51′S, 49°04′E, *Malcomber 1877* (CAN, DAV, G, K, MO, P, TAN, US).

Discussion. This species was discovered by the auther during a fieldtrip to the Ankarana Massif near the northern tip of Madagascar. The species was immediately distinguishable from the only species then known in Madagascar, *P. madagascariensis*, by its distinct gynoecium with styles entirely fused into an enlarged obovoid-obconic stylar column (Figs. 2E, 3B, D). Both *P. madagascariensis* and *P. decidua* have partly fused styles and a cylindrical stylar column (Figs. 3G, 4F). In addition, *P. ankaranensis* may be distinguished by its terminal leaf-opposed thyrse with moderately open cymes, distinctly winged ovaries, shorter styles (< 6 mm long), smaller staminate flowers with a shorter androecium (≤ 1 mm long), and absence of stipels or glandular knobs at the petiole apex. Capsules and seeds are larger than those of *P. decidua* (unknown for *P. madagasarensis*). Pollen grains are smaller than all other examined species of *Plukenetia*. The species shares with *P. madagascariensis* a similar leaf blade shape, inflorescence type (thryse) and length (~5–19 cm), and with *P. decidua*, terminal inflorescences and stamens 30 or fewer.

6. **Plukenetia decidua** L.J. Gillespie, sp. nov.—TYPE: Madagascar, Toliara, entre Ampanihy et Itrobiky, route Ampanihy-Androka, 4 Jul 1958, *Capuron*, *SF 18682* (holotype: P!; isotypes: P-2 sheets!). Fig. 4.

Plukenetia madagascariensis Leandri affinis, a quibus differt foliis ovatis vel triangularibus ovatis racemis brevioribus terminalibus floribus nodi singuli bracteis parvioribus eglandulatis antheris paucioribus.

Monoecious liana; stems glabrous, distinctly glaucous, sometimes twining; older branches slender, woody, greyish or mottled pale grey and tan, somewhat crooked and knobby with raised leaf scars. Stipules triangular, 0.4–1 mm long. **Leaves** deciduous; petioles 1.5–5 cm long, glabrous, distinctly glaucous; blades ovate or triangular-ovate, sometimes narrowly so, 3–6 × 1–4 cm, chartaceous, glabrous, acuminate at apex, obtuse, truncate or shallowly cordate at base with sinus to 0.5 cm

deep, margins distinctly serrulate; venation 3-nerved at base, secondary veins mostly semicraspedodromous, 4–8 on each side of midrib, tertiary veins percurrent; small glandular knob to 0.6 mm long, usually present between and just below basilaminar glands, sometimes absent; basilaminar glands 2, suborbicular, 0.8–1.3 mm in diam, prominent, above petiole apex; laminar glands absent or occasionally 1–3 per side, near margin towards apex. **Inflorescence** a narrow raceme, 3–7 cm long, bisexual, terminal at branch apex or sometimes on very short shoots, axes glabrous; peduncle usually absent (and pistillate flower basal); flowers 1 per node, pistillate flower 1 at basal-most node, staminate flowers numerous above; bracts triangular-ovate, 1–2 mm long, often with a small lobe on each side, margin whitish along lower half. **Staminate flower** pedicel 4–7 mm long, glabrous; bud ellipsoid, obtuse at apex; sepals 4, narrowly elliptic, 3–3.8 × ~1.5 mm wide, acute at apex, glabrous, open wide at anthesis; androecium ellipsoid or oblong-ellpsoid, 1.6–1.8 × 1.3–1.5 mm, comprising 18–30 sessile anthers on a narrowly stalked, ellipsoid receptacle, anthers densely packed proximally, sparser distally with apex often bare. **Pistillate flower** pedicel 4–5 mm long, glabrous; sepals narrowly triangular, 2–2.5 × 0.6–0.7 mm, glabrous; ovary 1.5–2.5 × 2–4 mm (including wings), glabrous, 4-winged, wings ~0.5 mm long; styles 8–11 mm long, glabrous, partly connate into a cylindrical column 4–6 × ~1 mm, the 4 free style arms 3.7–5 mm long, tapered apically, spreading, with their inner surface entirely stigmatic. **Fruit** a (1–)4-lobed capsule, 1.1–1.3 × 2.3–3.5 cm (immature?), glabrous, surface smooth and faintly reticulate, each carpel lobe carinate, keel widened centrally into horn-like wing to 10 mm long in immature fruit, ~2–2.5 mm long in mature fruit, styles to 12 mm long, persistent at least in immature fruit; pedicel 0.4–0.8 cm long. **Seeds** broadly ellipsoid, ~13 × 11–12 × 11–12 mm, ventral surface distinctly angular, dorsal surface rounded, surface (tegmen) densely minutely verrucate, dull pale orange-brown; testa not or partly persistent, white to purplish.

Pollen. Tricolpate, suboblate (P/E = 0.71–0.75), polar axis 32–35 μm, equatorial axis 44–51 μm; amb subcircular; colpus broad with margins uneven and jagged; exine ~2.5 μm thick, evenly thickened or somewhat thinner towards margin, tectum foveolate, smooth (voucher: *Capuron, SF 18682*).

Distribution and Ecology. Restricted to the southern tip of Madagascar (Fig. 5). A slender deciduous liana of dry scrub, ~20–250 m. Flowering when leafless or with young leaves. Flowering collections made in July, August, September, and November; fruiting collections made in August and December.

Specimens Examined. MADAGASCAR. **Toliara:** Source de Ranomay, Tangobory, *Capuron, SF 27952* (P); Antanimora, District d'Ambovombe, *Decary 2929* (P); Ambovombe, *Decary 3253* (P-2 sheets); Bassin inférieur du Mandrare, environs de Behara, *Humbert & Swingle 5664* (P-2 sheets); Réserve Naturelle Intégrale d'Andohahela, ENE Ihazofotsy, 24°49′00″S, 46°36′36″E, *Rakotomalaza 597* (CAN, MO, P, TAN, US).

Discussion. This is a distinctly deciduous, slender liana (also described as arbuste sarmenteux) that appears to flower prior to or simultaneously with the new flush of leaves. The distinctly glaucous branches and narrower ovate or triangular-ovate leaf blades are distinct from the other two species in Madagascar. The more prominent basilaminar glands are positioned together at the petiole apex, and usually have a small glandular knob between. Shorter narrow racemes with only one flower per node and glabrous axes and flowers also contrast with the longer thyrses, staminate flowers in cymules, and usually puberulous axes and flowers of the other two species. This species appears to be most closely related to *P. madagascariensis*, sharing a very similar style morphology.

Inflorescences are generally terminal at the ends of branches, but in one collection (*Decary 2929*) of a long twining branch they are terminal on very short shoots and appear almost axillary (with a leaf scar the only evidence of the subtending deciduous leaf).

The collection *Rakotomalaza 597* with immature and almost mature capsules is assigned to this species, but differs in two characters from other collections seen. The collection lacks the whitish waxy bloom characteristic of other collections examined (but preservation in alcohol may have dissolved the bloom). The mature leaves have truncate to cordate blade bases, compared to other collections which have obtuse-based leaves that appear to be immature or expanding. Otherwise the collection fits well within this species both morphologically and geographically.

7. PLUKENETIA MADAGASCARIENSIS Leandri, Bull. Soc. Bot. France 85: 527. Figs. 1.13–14. 1938.—TYPE: Madagascar, Prov. Mahajanga, Bois de Morataitra, rive droite de la Betsiboka, E de Maevatanana, Mar 1899, *Perrier 848* (lectotype, designated here: P!, isolectotypes: L!, P-2 sheets!). Fig. 3E–G.

Monoecious liana; stems glabrous, often twining; older branches thick, woody. Stipules triangular, 0.5–0.8 mm long. **Leaves** apparently deciduous;

petioles 2.5–8 cm long, glabrous or very sparsely pubescent; blades ovate or sometimes suborbicular, 4.5–10.5 × 4–7.5 cm, chartaceous, glabrous or glabrescent, slender acuminate to caudate at apex with tip 0.7–2 cm long, cordate, truncate, or rounded at base with sinus to 1 cm deep, margins crenulate-serrulate; venation 3-nerved at base or weakly palmate; secondary veins mostly craspedodromous, 3–5(–6) on each side of midrib; tertiary veins percurrent; knobs 1 or 2, often glandular, located between basilaminar glands; basilaminar glands 2, circular, 0.4–1 mm in diam, marginal or just above petiole apex; laminar glands absent. **Inflorescence** a spicate thryse, 6–19 cm long, bisexual or staminate, axillary, axes glabrous to sparsely pubescent; peduncle 0.5–4 mm long; pistillate flowers (0)1–2(3), 1 per node at basal-most node, staminate flowers numerous above in few-flowered cymules; cymules condensed, primary cyme axes 0.2–1.5 mm long; bracts lanceolate or linear-lanceolate, 3–8 mm long, glabrescent to moderately pubescent, attenuate at apex, petiolate, biglandular or rarely 4-glandular; bracteoles lanceolate or linear-lanceolate, to 3 mm long, eglandular or sometimes minutely biglandular. **Staminate flower** pedicel 5–10 mm long, glabrescent to moderately pubescent; buds narrowly ovoid or elliptic, bluntly acuminate, bluntly acute, or obtuse at apex; sepals 4, ovate or lanceolate, 3–6 × 1.5–2.5 mm, pale yellowish green to cream, very sparsely to moderately pubescent, attenuate and distinctly thickened at apex; androecium narrowly conical or narrowly ovoid-conical, 3–4 × 0.9–1.2 mm, comprising 35–60+ sessile yellow anthers loosely packed on shortly stalked, narrowly conical, pale green receptacle. **Pistillate flower** pedicel 2–2.5 mm long, sparsely to moderately pubescent; sepals lanceolate or ovate, 2.5–4 × ~1.4 mm, green, sparsely to moderately pubescent; ovary ~2 mm in diam, verrucose, pubescent, not distinctly winged or horned; styles 10–16(–22 according to Perrier) mm long, green, partly connate into a cylindrical column 6–8(–12) × ~1 mm, the four free style arms 4–8(–10) mm long, tapered apically. **Fruit** and **seeds** not seen.

Pollen Description. Gillespie (1994).

Illustration. Leandri (1938), Figs. 1.13–14.

Distribution and Ecology. Widespread, but with a scattered distribution in western Madagascar, from east of Analalava to just north of Toliara (Fig. 5). A slender liana found in open areas in dry forest on limestone or sandy soils (Fig. 3E), 20–600 m. Plants are apparently deciduous during the dry season, with new leafy shoots produced in December (November to January) at the beginning of the wet season. Flowering specimens were collected between January and April, when either new or mature leaves were present.

Specimens Examined. MADAGASCAR. **Mahajanga:** Tsingy de Bemaraha, E Antsalova, *Cremers 3771* (P-5 sheets); Réserve Naturelle Bemaraha, Ambodiriana (campement at river crossing along Antsalova-Ambondro track), ~9 km E of Antsalova, 18°39′S, 44°43′E, *Gillespie 4144* (CAN, MO); 1–3 km SW of Antseranandraka, along road to Ambareny, between Lake Bemaraha and Lake Masama, ~30 km SW of Antsalova, 18°50′S, 44°24′E, *Gillespie 4175* (CAN, K, MO, TAN); Antsingy d'Antsalova, Reserve Natural Bemaraha (RN 9, *Morat 4893* (P, TAN); Haute Sofia, près d'Antoakabary, 600 m, Nov 1922, *Perrier 15078* (syntype: P!). **Toliara:** Lambobe River, ~6 km N of Beroboka, 55 km NE of Morondava, 19°54′S, 44°36′E, *Gillespie 4125* (CAN, K, MO, NY, P, TAN, US); Route N9, km 37–39, near Andrevo, 23°03′S, 43°35′E, *Mabberley 965* (K); Belalanda Commune, Ranobe, 23°00′46″S, 43°39′09″E, *Andrianjafy et al. 1648* (P, photos seen).

Discussion. This species may be distinguished by its elongate androecium (2.5–4 mm long) with many anthers (35–60), and relatively large (3–8 mm long) inflorescence bracts, which are often petiolate and biglandular. The presence of petiolate biglandular bracts is unique in *Plukenetia*, all other species having smaller, eglandular, usually narrowly triangular bracts. The species may also be distinguished from other members of the Madagascan species complex by its axillary inflorescences and specifically from *P. ankaranensis* by its longer, partly connate styles (Fig. 3G) and one or two small glandular knobs at the petiole/blade junction, and from *P. decidua* by its broader leaf blades (Fig. 3F), longer inflorescences, and longer styles.

The species shares with *P. decidua* a very similar style morphology of styles connate for one half to two thirds of their length into a cylindrical stylar column with tapered free style arms (Figs. 3G, 4F). Similar style morphology is present only in the neotropical species *P. lehmanniana* (styles arms are less tapered and blunt-tipped) (Gillespie 1993, Fig. 1A). Other paleotropical species with partly connate styles have either much shorter styles or mostly connate styles with short dilated arms.

Several characters appear to be somewhat variable in the species. Inflorescence axes may be sparsely pubescent (collections from Bemeraha area) or glabrous. The two basilaminar glands on the adaxial surface of the leaf blade may be located either along the margin near the base or just above the petiole apex, with either one or two knobs between. Further collections are needed to determine if this variation has a geographical basis and to ascertain if this is a single variable species or if more than one taxon should be recognized.

Excluded Species

Plukenetia zenkeri Pax, Bot. Jahrb. Syst. 43: 83. 1909. = *Hamilcoa zenkeri* (Pax) Prain, Bull. Misc. Inform. Kew. 1912: 107. Fig. p.984. 1912.

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