

A Contribution to the Guianan  
Flora: *Dalechampia*, *Haematostemon*,  
*Omphalea*, *Pera*, *Plukenetia*,  
and *Tragia* (Euphorbiaceae)  
with Notes on Subfamily Acalyphoideae

*Lynn J. Gillespie*  
and *W. Scott Armbruster*



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## ABSTRACT

Gillespie, Lynn J., and W. Scott Armbruster. A Contribution to the Guianan Flora: *Dalechampia*, *Haematostemon*, *Omphalea*, *Pera*, *Plukenetia*, and *Tragia* (Euphorbiaceae) with Notes on Subfamily Acalyphoideae. *Smithsonian Contributions to Botany*, number 86, 48 pages, 14 figures, 1997.—*Dalechampia*, *Haematostemon*, *Omphalea*, *Pera*, *Plukenetia*, and *Tragia* (Euphorbiaceae, subfamily Acalyphoideae) are treated for the Guianas. Notes on Guianan Euphorbiaceae, subfamily Acalyphoideae, tribes Omphaleae, Pereae, and Plukenetiae, and ecological notes on each species are given. Also included is a key to the subfamilies of Euphorbiaceae and a key to the Guianan genera of subfamily Acalyphoideae.

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Flora: *Dalechampia*, *Haematostemon*  
*Omphalea*, *Pera*, *Plukenetia*,  
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with Notes on Subfamily Acalyphoideae

*Lynn J. Gillespie*  
*and W. Scott Armbruster*

**Introduction**

This contribution treats three of the 10 tribes of subfamily Acalyphoideae known from the Guianas. Tribe Plukenetiae includes four genera in the Guianas, whereas the remaining two tribes, Omphaleae and Perea, each comprise a single genus. A more concise version of this contribution eventually will be published as part of the Euphorbiaceae treatment for the *Flora of the Guianas*. However, only a very small part of the Guianan Euphorbiaceae currently is under study, and there is no scheduled completion date for the family treatment. No further work by the two authors on the taxonomy of Euphorbiaceae of the Guianas is anticipated at present. Current interest in the Guianan flora and the need for up-to-date treatments of neotropical taxa make it timely to publish the completed study of these tribes at this time.

This treatment is limited to the three Guianan countries, Guyana, Surinam, and French Guiana. Species from neighboring areas within the Guayana Region also are included or mentioned if they are thought likely to occur in the Guianas. The Guayana Region (Gillespie, 1993a; equivalent to the Guayana Lowland Floristic Province as defined by Mori, 1991) is a more biogeographically natural region than the Guianas

and includes, in addition to the Guianas, the Venezuelan Guayana (comprising the states of Amazonas, Bolívar, and the Delta Amacuro) and Amazonian Brazil north of the Amazon and Negro rivers.

In addition to the floristic taxonomic treatments of the genera *Dalechampia*, *Haematostemon*, *Omphalea*, *Pera*, *Plukenetia*, and *Tragia*, we have included notes on Guianan Euphorbiaceae, subfamily Acalyphoideae, and tribes Omphaleae, Perea, and Plukenetiae. Also included are keys to the five subfamilies of Euphorbiaceae and to the 18 genera of Acalyphoideae known from the Guianas.

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**EUPHORBIACEAE in the Guianas**

The Euphorbiaceae is considered to be the fifth largest flowering plant family and comprises about 300 genera and 7500 species. Forty-eight genera and 171 species are known to

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be indigenous or extensively naturalized in the Guianas, whereas an additional six genera and 22 species are known only in cultivation or are naturalized to a very limited extent in the Guianas (Gillespie, 1993a; additions to checklist listed below). Twenty-one species (12%) of Guianan Euphorbiaceae are strictly endemic to the Guianas, whereas 55 species (32%) are endemic to the more broadly defined Guayana Region (Gillespie, 1993a, with additional species listed below).

Five new species have been described from the Guianas since publication of the most recent checklist of Guianan Euphorbiaceae (Gillespie, 1993a). These are *Dalechampia brevicolumna* Armbruster, *D. heterobracteata* Armbruster (Armbruster, 1996), *Mabea salicoides* Esser (Esser, 1993), *Plukenetia supraglandulosa* L.J. Gillespie (Gillespie, 1993b), and *Tragia tabulaemontana* L.J. Gillespie (Gillespie, 1994b). New records for the Guianas include *Croton draconoides* Muell. Arg. (Hoff et al., 1996), *Dalechampia olympiana* Kuhlman & Rodrigues (Armbruster, 1996), *Manihot* aff. *quinquepartita* Rogers and Appan (Gillespie, unpublished data), *Phyllanthus caribeus* Urb. (Webster, pers. comm., 1993), and *Senefeldersopsis croizatii* Steyerem. (Esser, 1995). Additionally, three species of *Dalechampia*, *D. stipulacea* Muell. Arg., *D. aff. cissifolia*, *D. aff. triphylla*, that are new to the Guianas are presented here.

Previous floras and checklists of Euphorbiaceae of the Guianas include *The Euphorbiaceae of Surinam* (Lanjouw,

1931; additions by Görts-van Rijn, 1976), *Flore de la Guiane Française* (Lemée, 1952), and *Checklist of Woody Plants of Guyana* (Mannega et al., 1988). The series *Botany of the Guayana Highland* (Jablonski, 1965, 1967) treats the Euphorbiaceae flora of the region adjacent to the western border of Guyana, as will the Flora of the Venezuelan Guayana (Steyermark et al., 1995; Webster et al., in prep). Additional references, including recent revisionary studies of neotropical Euphorbiaceae, are listed in Gillespie (1993a).

Five subfamilies of Euphorbiaceae are currently recognized (classification of Webster, 1975, 1994). The family previously was divided into two major groups based on the number of ovules per locule, the biovulate taxa belonging to the Phyllanthoideae sensu Pax and the uniovulate taxa to the Crotonoideae sensu Pax (Pax, 1890; Pax and Hoffmann, 1931; for an historical account refer to Webster, 1987). In Webster's classification two subfamilies, Phyllanthoideae and Oldfieldioideae, include all biovulate taxa, whereas the remaining three subfamilies, Acalyphoideae, Crotonoideae sensu Webster, and Euphorbioideae, comprise all uniovulate taxa.

All five subfamilies of Euphorbiaceae occur in the Guianas. The largest subfamily in the Guianas (excluding cultivated genera and species) is the Acalyphoideae (17 genera, 54 species), followed by the Crotonoideae (11 genera, 50 species), Euphorbioideae (11 genera, 35 species), Phyllanthoideae (8 genera, 31 species), and Oldfieldioideae (1 genus, 1 species).

### Key to the Subfamilies of Euphorbiaceae in the Guianas

1. Ovules paired in each locule of the ovary; fruit with 1–10 (often 6) seeds, 1 or 2 in each locule; staminate calyx-lobes imbricate in bud; latex absent; leaf (or leaflet in *Piranhea*) blade pinnately veined, the margins unlobed, entire, or obscurely crenate; leaf lacking petiolar glands and usually lacking embedded laminar glands; indumentum simple or lepidote . . . . . 2
- Ovules solitary in each locule of the ovary; fruit with 1–3 (rarely to 20) seeds, always solitary in each locule; staminate calyx-lobes valvate, imbricate, reduced, or absent; latex present or absent; leaf blade pinnately or palmately veined, the margins often lobed, serrate, or dentate; leaf often with petiolar glands and/or embedded laminar glands; indumentum simple, lepidote, stellate, or dendritic . . . . . 3
2. Leaves simple; seeds ecarunculate; herbs, shrubs, or trees [*Podocalyx* of subfamily Oldfieldioideae keys out here, but known only from the Guayana Region outside of the Guianas] . . . . . Subfamily **PHYLLANTHOIDEAE**
- Leaves trifoliate; seeds carunculate; dioecious trees [*Piranhea*, is the only genus in the Guianas.] . . . . . Subfamily **OLDFIELDIOIDEAE**
3. Staminate bracts biglandular at base (except *Hura* and *Senefeldera*) or inflorescence cyathial (i.e., flowers contained within a cupular cyathium formed by 5 connate bracts); staminate calyx-lobes imbricate, reduced, or absent, usually not covering the anthers in bud; petals absent; floral disc (nectary) absent; leaf blades simple, pinnately veined, unlobed; indumentum, if present, simple or dendritic (in *Mabea* spp. and *Senefeldera* spp.); latex milky white, sometimes scant or rarely absent . . . . . Subfamily **EUPHORBIOIDEAE**

- Staminate bracts eglandular (except *Omphalea* and *Pausandra*), inflorescence not cyathial; staminate calyx-lobes valvate or imbricate, covering the anthers in bud; petals present or absent; floral disc present or absent; leaf blades simple or compound, pinnately or palmately veined, lobed or unlobed; indumentum simple, stellate, or lepidote; latex clear, colored, milky white, or absent . . . . . 4
4. Petals present at least in staminate flowers (if absent then sepals petaloid or latex present); latex milky white, colored, clear, or rarely absent; petiolar glands often present; staminate calyx-lobes mostly imbricate in bud; styles bifid or multifid (entire in *Aleurites* and *Codiaeum*, both cultivated genera), free or connate only at base; seeds mostly carunculate; pollen with crotonoid exine sculpture (clavae arranged in regular hexagonal pattern) . . . . . Subfamily **CROTONOIDEAE**
- Petals absent (present in *Caperonia* and *Pogonophora*); latex absent (pinkish to red in *Omphalea*); petiolar glands absent (present in *Omphalea*); staminate calyx-lobes mostly valvate in bud; styles entire to multifid, free to entirely connate; seeds mostly ecarunculate; pollen never with crotonoid exine sculpture . . . . . Subfamily **ACALYPHOIDEAE**

**Subfamily ACALYPHOIDEAE**

The Acalyphoideae, with 116 genera in 20 tribes, is the largest and most complex subfamily in the Euphorbiaceae (Webster, 1994). Species characteristically lack latex, petiolar glands, inflorescence bract glands, and petals, and they typically have staminate flowers with valvate sepals. The subfamily is not defined by any uniquely derived character or character complex, but instead it is characterized primarily on the basis of characters considered plesiomorphic in the Euphorbiaceae (with the exception of apetalous flowers, a state that appears to have evolved several times in the family). As currently circumscribed, the Acalyphoideae is paraphyletic, comprising all uniovulate taxa that do not fit in either the Crotonoideae or Euphorbioideae. Although a large group of related genera appears to form the core of the subfamily (e.g., tribes Acalypheae and Alchornieae), there are many genera that appear to be phylogenetically isolated (e.g., *Chaetocarpus* Thwaites, *Clutia* L., *Omphalea*, *Pera*, and *Pogonophora* Miers ex Benth.).

In Acalyphoideae five tribes are unigeneric, whereas three comprise only two genera. The largest tribe is the Acalypheae

with 30 genera. Eighteen genera (including the cultivated genus *Ricinus*) in 10 tribes of Acalyphoideae are known from the Guianas. In addition, the genus *Acidoton*, known from neighboring Bolivar state, Venezuela, may be expected to occur in the Guianas and is included in the key to genera.

DESCRIPTION.—Trees, shrubs, herbs, or vines; monoecious or dioecious; latex absent or rarely present and then not milky white; indumentum simple, lepidote, or stellate. Leaves simple or rarely palmately compound, alternate or rarely opposite, usually stipulate; blades pinnately or palmately veined, margin entire, serrate, or lobed; petiolar glands absent (present in *Omphalea*), laminar glands often present. Inflorescence various; bracts eglandular (biglandular in *Omphalea*). Flowers lacking corolla (except *Caperonia* and *Pogonophora*); disc present or absent. Staminate calyx mostly valvate or sometimes imbricate, anthers covered in bud; pollen grains 3(-4)-colporate or -colpate, rarely porate or inaperturate, exine tectate, semitectate, or rarely intectate, never with crotonoid exine sculpture. Ovary 3-locular, rarely 1-, 2-, or 4-locular, ovules solitary in each locule; styles entire to multifid, free to entirely connate. Fruit capsular or rarely baccate; seeds (1-)3(-4), solitary in each locule, mostly ecarunculate; testa mostly dry, sometimes fleshy.

**Key to the Genera of Acalyphoideae in the Guianas**

1. Petals present in both staminate and pistillate flowers; staminate flower with pistillode . . . . . 2
- Petals absent from both staminate and pistillate flowers; staminate flower with or without pistillode . . . . . 3
2. Leaf blade margins entire, the secondary veins arcuate; stamens 5; dioecious trees . . . . . *Pogonophora*
- Leaf blade margins finely serrate, the secondary veins closely set and distinctly parallel; stamens 10; monoecious herbs . . . . . *Caperonia*

3. Inflorescences pseudanthial, the flowers subtended by an involucre of 2 free or connate bracts, the involucre usually showy, sometimes reduced . . . . . 4  
 Inflorescences not pseudanthial . . . . . 5
4. Flowers enclosed within globose, petal-like involucre, consisting of 2 connate bracts, opening along one side at anthesis; involucre unisexual, in axillary clusters on woody branches below leaves; leaves simple, blade not lobed; dioecious trees . . . . . 2. *Pera*  
 Flowers subtended by bilabiate involucre of 2 palmately veined foliaceous or stipuliform bracts; involucre bisexual, axillary or terminal on short shoots; leaves simple to palmately compound, blade often lobed; monoecious twining vines or rarely shrubs . . . . . 3. *Dalechampia*
5. Stamens 100–1000, the filaments partly and irregularly connate; leaf blade peltate, palmately 7- to 11-lobed; inflorescence bisexual, the pistillate flowers numerous and distal; seeds carunculate; monoecious, weak-stemmed shrubs, cultivated in the Guianas . . . . . *Ricinus*  
 Stamens 2–60, filaments free to completely connate; leaf blade not peltate, rarely lobed; inflorescence unisexual or bisexual with pistillate flowers proximal; seeds mostly ecarunculate . . . . . 6
6. Flowers in axillary glomerules; staminate sepals imbricate in bud; capsule spiny-tuberculate; seeds black, shiny, with large red caruncle; dioecious shrubs or small trees . . . . . *Chaetocarpus*  
 Flowers in spicate, racemose, or paniculate inflorescences (terminal glomerules in *Bernardia*); staminate sepals valvate in bud (imbricate in *Omphalea*); capsule not spiny-tuberculate; seeds ecarunculate or rarely with very small caruncle, usually not black . . . . . 7
7. Androecium mushroom-shaped, the stamens 2, completely connate, with connective greatly expanded; staminate sepals imbricate in bud; inflorescence terminal, paniculate, the cymules bisexual or staminate; bracts usually large, foliaceous, petiolate; latex red, sometimes scant; monoecious lianas . . . . . 1. *Omphalea*  
 Androecium not mushroom-shaped, the stamens 2–60, free or connate only at base, connective not or only slightly expanded; staminate sepals valvate in bud; inflorescence axillary or terminal, spicate or racemose, the cymules unisexual or flowers solitary at a node; bracts small, not foliaceous (large sessile bracts often subtend pistillate flower(s) in *Acalypha*); latex absent or rarely present and then not colored . . . . . 8
8. Styles entire, basally to completely connate, often massive; inflorescence usually bisexual with 1 to several basal pistillate flowers; plants often twining vines (if not then urticating hairs present or styles completely connate and massive), sometimes with urticating hairs, monoecious (dioecious in *Acidoton*) . . . . . 9 [Tribe Plukenetieae]  
 Styles branched or entire, free or sometimes basally connate (rarely long-connate and then bifid), not massive, rarely absent; inflorescence unisexual (sometimes bisexual in *Acalypha* and *Bernardia* and then the styles branched); plants not twining vines, lacking urticating hairs, dioecious (usually monoecious in *Acalypha* and *Bernardia*) . . . . . 12
9. Ovary 4-locular; fruit 4-lobed or subglobose, dehiscent or indehiscent; leaf blade with circular laminar glands at base; twining vines or lianas lacking urticating hairs . . . . . 5. *Plukenetia*  
 Ovary 3-locular; fruit 3-lobed, dehiscent; leaf blade lacking laminar glands; habit various, urticating hairs present or absent . . . . . 10
10. Urticating hairs absent; sepals 4; stamens 4; styles completely connate forming a massive hollow cup-shaped structure; leaf blades pinnately veined; monoecious shrubs or trees . . . . . 4. *Haematostemon*



- Urticating hairs present at least on ovary and capsule; sepals 3 or 5; stamens (1-)3 or numerous; styles slender, only partly connate; leaf blades pinnately or palmately veined . . . . . 11
11. Anthers with apical tuft of urticating hairs; leaves glabrescent, pinnately veined; dioecious shrubs or trees . . . . . *Acidoton*  
 Anthers not apically tufted; leaves with urticating hairs or rarely glabrescent, pinnately or palmately veined; monoecious twining vines (in the Guayana Region) . . . . . 6. *Tragia*
12. Styles lacinate (i.e., multifid with many filiform segments); pistillate bracts usually large, conspicuous, and lobed; anthers vermiform (elongate and worm shaped); inflorescence spicate; herbs, shrubs, or small trees, mostly monoecious . . . . . *Acalypha*  
 Styles entire or bifid, not lacinate; pistillate bracts small and inconspicuous; anthers not vermiform, usually globose or ellipsoid; inflorescence various; habit various, mostly dioecious . . . . . 13
13. Pistillate or bisexual inflorescence glomerate, terminal; staminate inflorescence, if present, spicate or racemose, shorter than 5(-6) cm; stamens 4-6, the anthers constricted at middle, having the appearance of 4 globose locules; styles stout, short, free, bipartite to base; leaf blade shorter than 10(-12) cm, usually hirsute, the margins coarsely serrate; herbs or weak-stemmed shrubs . . . . . *Bernardia*  
 Pistillate and staminate inflorescences spicate, racemose, or paniculate, longer than 5 cm, axillary or terminal; stamens 2-60, the anthers not constricted; styles various; leaf blade usually longer than 10 cm, rarely hirsute, the margins entire to serrulate; shrubs or trees . . . . . 14
14. Stamens 15 or more; styles bifid; capsules ovoid or pear-shaped, mostly circular in cross section, greater than 1.5 cm in diameter; leaf blades palmately or pinnately veined; hairs minutely stellate . . . . . 15  
 Stamens fewer than 10; styles entire, indistinctly bifid, or absent; capsules subglobose to oblate, lobed in cross section, less than 1.5 cm in diameter; leaf blades pinnately veined (either 1 or 3-veined at base); hairs simple or minutely stellate . . . . . 16
15. Carpels 2, styles 2; pistillate calyx cup-shaped, only slightly lobed; staminate inflorescence axillary; all stamens fertile; pistillode present; leaf blade narrowly obovate . . . . . *Gavarretia*  
 Carpels 3, styles 3; pistillate calyx deeply lobed into sepals; staminate inflorescence terminal; inner stamens often sterile; pistillode absent; leaf blade cordiform, ovate, or elliptic . . . . . *Conceveiba*
16. Styles absent (i.e., stigmas sessile); stamens 2(-3); leaf blades 1-veined and narrowly cuneate at base, eglandular . . . . . *Adenophaedra*  
 Styles present; stamens 3-8; leaf blades 1- or 3-veined at base, acute to rounded at base, usually with laminar glands . . . . . 17
17. Carpels 2; styles 2; elongate, slender, free; stamens usually 8, pistillode absent; hairs minutely stellate . . . . . *Alchornea*  
 Carpels 3; styles 3, short, free or connate at base; stamens 3-8, pistillode present or absent (if stamens 8, then pistillode present); hairs simple . . . . . 18
18. Staminate flower with large pubescent pistillode, 5-8 stamens, the anthers apiculate; pistillate flowers sessile; capsule ~5 mm in diameter; outer seed coat fleshy, bright red; leaf blades less than 15 cm long, distinctly 3-veined and without stipels at base . . . . . *Alchorneopsis*  
 Staminate flower without pistillode, with 3-5 stamens, the anthers not apiculate; pistillate flowers with pedicel longer than 4 mm; capsule ~1 cm in diameter; outer seed coat dry, brownish; leaf blades usually longer than 15 cm, distinctly 1-veined and with pair of stipels at base . . . . . *Aparisthium*

### Tribe OMPHALEAE

Tribe Omphaleae (Pax & Hoffm.) Webster, is anomalous in the Acalyphoideae in having latex, biglandular petioles, usually biglandular inflorescence bracts, and imbricate sepals. The tribe shares the above characters with subfamily Euphorbioideae, but it differs in having palmately veined, sometimes lobed leaves, and in having pinkish to red rather than milky white latex. With the exception of biglandular bracts, the tribe shares the same characters with the Crotonoideae, but it does not have pollen with a crotonoid exine sculpture, a diagnostic character of that subfamily (known to be absent in only a single species of *Micrandra*; Nowicke, 1994). This heterogenous mix of subfamilial characters and the lack of any closely related taxa indicates that the Omphaleae most likely represent a rather ancient lineage within the uniovulate euphorbs. A single genus comprises tribe Omphaleae.

*Omphalea* is distributed pantropically, except for most of mainland Africa, with centers of diversity and endemism in Madagascar and the Caribbean. This peculiar, somewhat relictual distribution may perhaps be further evidence of its antiquity. *Omphalea* may be distinguished by its unusual mushroom-shaped androecium, pinkish to red latex, foliaceous inflorescence bracts, and usually large paniculate inflorescences of bisexual or staminate cymes.

#### 1. Genus *Omphalea* L.

*Omphalea* L., Syst. nat., ed. 10, 2:1264, 1759. [Type: *Omphalea triandra* L.]

DESCRIPTION.—Trees, shrubs, or lianas, monoecious; latex red or pink, scant to copious; indumentum of simple hairs. Leaves simple, petiolate; stipules small, deciduous; blade margin entire to deeply lobed, pinnately or palmately veined; pair of glands present at petiole apex or blade base; laminar glands usually scattered on abaxial surface of blade. Inflorescence a terminal thyrse, appearing spicate, racemose, or paniculate; cymose subunits bisexual with central flower(s) pistillate or distally unisexual and all staminate; bracts subtending cymose subunits large, leaf-like, often biglandular; bracteoles small, triangular, usually eglandular. Staminate flowers pedicellate; sepals 4–5, imbricate; corolla absent; disc extrastaminal, annular, rarely 5-segmented or absent; androecium mushroom-shaped with massive hemispheroidal cap formed from highly expanded connate anther connectives, or rarely not mushroom-shaped with anthers free and connectives not expanded; filaments completely connate into a usually slender staminal column or rarely anthers subsessile; anthers 2 or 3; pistillode absent. Pistillate flowers subsessile to pedicellate; sepals 4–5, imbricate; corolla and disc absent; ovary 3-locular; styles completely connate, usually massive. Fruit a 3-seeded schizocarpic capsule or berry; capsule separating into

3 mericarps, the mericarps fleshy or woody, indehiscent or loculicidally dehiscent. Seeds globose, ovoid, or ellipsoid, ecarunculate, surface smooth, roughened, or tuberculate.

DISTRIBUTION.—Seventeen species, pantropical; one species in the Guianas.

LITERATURE.—Pax and Hoffmann (1912); Gillespie (1988).

#### 1. *Omphalea diandra* L.

##### FIGURE 1

*Omphalea diandra* L., Syst. nat., ed. 10, 2:1264, 1759. [Type: none designated.]

*Omphalea megacarpa* Hemsley, Hooker's Icon, pl. 4, pl. 2537, 1897. [TYPE: Tobago, *Gilloway TRIN 5071* (holotype, K!).]

DESCRIPTION.—Liana to 30 m or more in forest canopy, climbing by means of tendril-like stems; trunk cylindrical, up to 20 cm in diameter; growth sympodial. Petiole 4–20 cm long; blade chartaceous to subcoriaceous, ovate or elliptic, 15–27 × 6–16 cm, apex rounded-acuminate or obtuse-acuminate, base shallowly cordate or rounded, glabrescent to velutinous below, margin entire, laminar glands scattered near margin below; pair of glands present adaxially at petiole apex. Inflorescence a paniculate thyrse, 15–65 cm long, cymes condensed, axes sparsely to densely pubescent; bracts to 6 cm long, petiolate, biglandular, blade oblanceolate or narrow elliptic, to 5 × 0.8 cm. Staminate pedicel 1–4 mm long; sepals 4 or rarely 5, subspherical or broadly ovate, 1.5–3.5 mm long; disc annular; androecium mushroom-shaped, staminal column slender, cap 1–2 mm in diameter, anthers 2. Pistillate pedicel 0.2–2.3 mm long; sepals 4 or 5, subspherical or broadly ovate, 1.5–2.5 mm long; ovary globose, 2–3.5 mm in diameter, densely pubescent; style subglobose, 1.6–2.6 mm in diameter, densely pubescent. Fruit subglobose, 8–12 cm in diameter, indehiscent; pericarp fleshy leathery, shiny green or greenish yellow. Seeds 3, broadly ellipsoid, radially compressed, 3.4–4.8 × 3.3–5 × 2.2–3.2 cm, surface dark brown, rough, dull; testa 0.5–2 cm thick, fleshy, white, not persistent.

DISTRIBUTION.—Widespread in the Neotropics, from Honduras and the West Indies to Bolivia and Brazil; ~160 collections examined, of which 67 are from the Guianas (Guyana: seven collections, Surinam: 34 collections, and French Guiana: 26 collections; abbreviated hereafter as G:7, S:34, FG:26).

ECOLOGY.—Canopy liana in moist to wet lowland forest, below 700 m (below 500 m in the Guianas), often dispersed and uncommon, but sometimes locally abundant in riparian forest, littoral forest, or at edge of granitic outcrops (e.g., Voltzberg). Flowers mostly between June and December in the Guianas. Seed germination is epigeal and cryptocotylar, i.e., the cotyledons of seedlings are above ground but remain hidden within the seed coat (Gillespie, 1988). This is an unusual mode

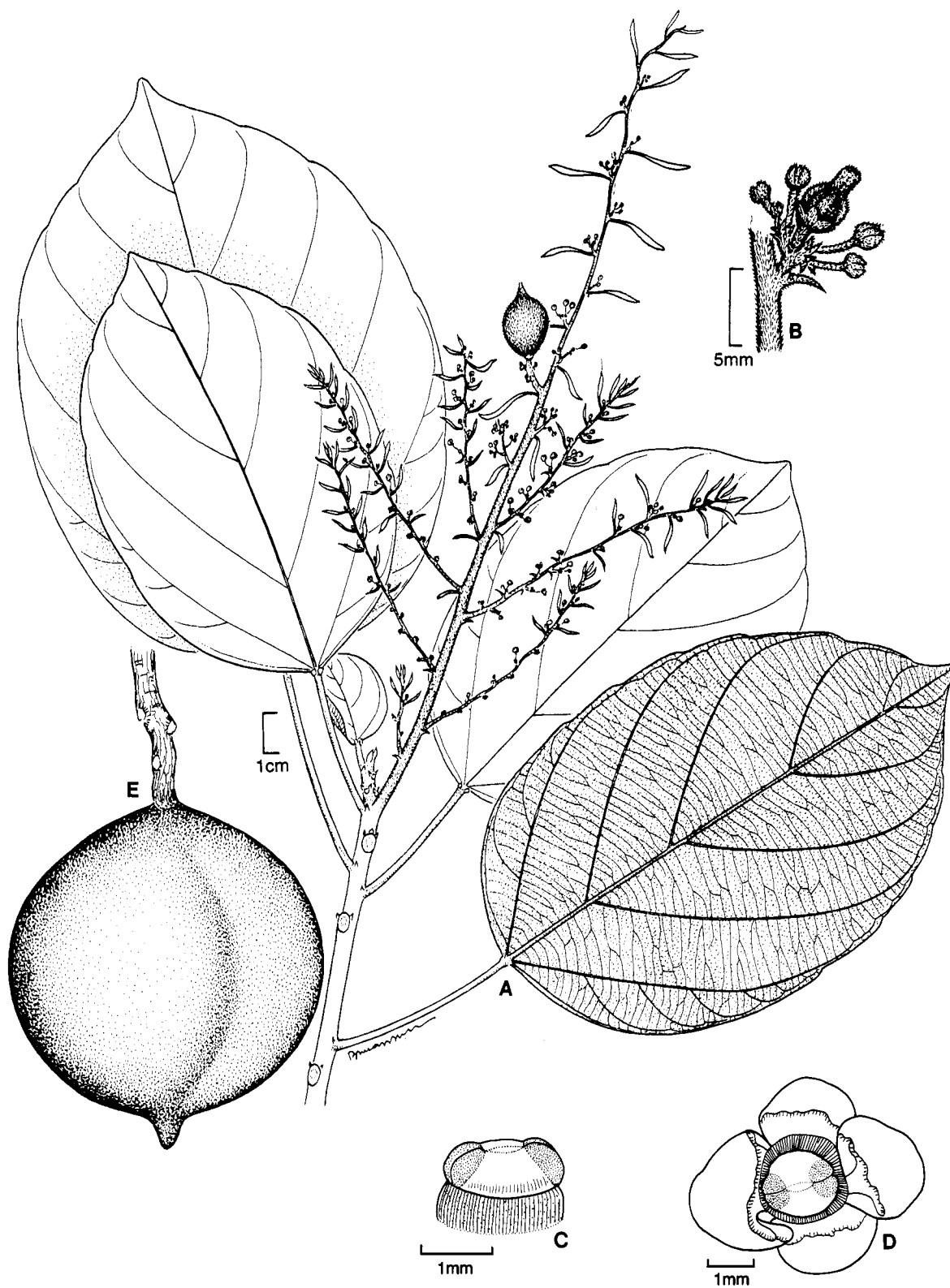


FIGURE 1.—*Omphalea diandra* L.: A, habit, flowering branch; B, cymose partial-inflorescence showing central pistillate flower and outer staminate flower buds; C, androecium above annular nectary; D, staminate flower at anthesis; E, fruit (A,B,E based on Gentry *et al.* 30692; C,D based on Gillespie 648).

of germination in the Euphorbiaceae, where the majority of species have seedlings with cotyledons that emerge from the seed coat and are green and photosynthetic.

SELECTED SPECIMENS EXAMINED.—Guyana: Pomeroon River, *de la Cruz 3186* (F, GH, MO, NY, UC, US); Groete Creek, Lower Essequibo River, *Fanshawe 1993 = FD 4729* (A, FDG, K, NY, U). Surinam: Beach N of Galibi, mouth of Marowijne River, *Lanjouw & Lindeman 1045* (NY, U); Lucie River, 2–10 km below confluence of Oost River, *Irwin et al. 55556* (F, K, MO, NY, U, US, VEN); Voltzberg, *Lanjouw 867* (MO, S, U). French Guiana: Rio Oiapoque, Roche Mon Pere, *Irwin et al. 48181* (MO, NY, U, UC, US, VEN); Ile de Cayenne, Pointe de Bourda, *Granville 5753* (U).

VERNACULAR NAMES.—Surinam: baboenoot, baboenotto, idaballie (Arawak), mekoekwaire, sitjo (Carib). French Guiana: ouabé, sooke (Taki-Taki), graine de l'anse, liane papaye.

USES.—Seeds are reported as edible but may be mildly toxic unless the embryo is removed. Oil extracted from the seeds has been used medicinally as a purgative (Freeman and Williams, 1927). In the Guianas, necklaces apparently have been made out of small polished fragments of the hard seed coat (Duss, 1897).

NOTES.—Mature individuals of *Omphalea* are large canopy lianas with one or more cylindrical trunks, whereas young individuals are vine-like. The genus is unique among Guianan Euphorbiaceae in having a liana habit combined with an unusual mode of climbing. Only the distal leafless part of the main stem twines and functions in climbing. These distal twining stem sections soon abort and frequently appear tendril-like following further growth of the axis from a sympodial shoot at their base. This method of climbing is in contrast to the much more typical method of all other Euphorbiaceae vines and lianas in the Guianas (e.g., *Dalechampia* spp., *Plukenetia*, and *Tragia*). These species climb by means of twining stems that both bear leaves and continue to grow.

Leaf shape, texture, and pubescence can vary considerably depending on maturity of plant and position on plant. Typical mature leaves of *O. diandra* are ovate, subcordate at base, subcoriaceous, and usually pubescent below, whereas juvenile leaves are lanceolate, rounded or obtuse at base, membranous-chartaceous, and glabrescent. Leaves from shady understory habitats or new lateral shoots from old branches frequently resemble juvenile leaves (e.g., *Lindeman 5111*).

### Tribe PEREAE

Tribe Pereae (Klotzsch & Gcke.) Pax & K. Hoffm. is unique in the Euphorbiaceae in having unisexual pseudanthia consisting of morphologically reduced flowers enclosed by a showy, more or less globose, involucre. Pseudanthia are frequently strongly scented, and the bracts are typically yellow,

cream, white, or sometimes red in color. Tribe Pereae represents one of three independent origins of pseudanthia in the Euphorbiaceae; pseudanthia also characterize *Dalechampia* and tribe Euphorbieae (i.e., the cyathium of *Euphorbia* L. and related genera).

Tribe Pereae includes only the single genus *Pera*. The highly reduced nature of the flowers has to a large degree obscured its phylogenetic affinity. Airy Shaw (1973) in recognizing the genus as a distinct family, the Peraceae, emphasized its isolated position (also discussed by Radcliffe-Smith, 1987). Most recently, Webster (1994) suggested that *Pera* may be most closely related to tribe Chaetocarpeae based on similarity in pollen, capsule, and seed morphology (e.g., they share carunculate seeds, an unusual character in subtribe Acalyphoidae).

### 2. Genus *Pera* Mutis

*Pera* Mutis, Kongl. Svenska Vetensk. Acad. Handl., 5:299, t. 8, 1784. [Type: *Pera arborea* Mutis.]

DESCRIPTION.—Shrubs or trees; dioecious (or rarely monoecious); indumentum usually of lepidote (flat peltate scale-like) or stellate hairs, rarely of simple hairs. Leaves simple, alternate or rarely opposite, petiolate, exstipulate, eglandular; blade pinnately veined, secondary veins looped, margin entire. Inflorescence pseudanthial, unisexual (or rarely bisexual?); pseudanthial units pedunculate, fasciculate on short shoots from woody branches either below the leaves or in axils of older leaves, comprising 3 or 4 flowers subtended by a showy involucre and (1–)2 bracteoles; involucre subglobose, ovoid, or ellipsoid, consisting of two connate bracts, completely enclosing flowers in bud, at anthesis opening along one side only and usually remaining subglobose or rarely opening wide; staminate pseudanthia sometimes with pistillodes representing reduced pistillate flowers, pistillate pseudanthia sometimes with rudimentary calyx(ces) representing reduced staminate flower(s). Staminate flowers sessile; calyx present, reduced, or absent, lobed or lacinate; corolla and disc absent; stamens (2–)3–4; filaments slender or stout, usually connate at base. Pistillate flowers sessile or shortly pedicellate; calyx, corolla, and disc absent; ovary 3-locular; styles absent or very short and connate; stigmas 3, sessile or subsessile, connate into thick peltate structure. Fruit a 3-seeded schizocarpic capsule, globose or ellipsoid, dehiscent into 3 woody cocci; columella slender, usually not persistent. Seeds ovoid to ellipsoid, radially compressed, carunculate, surface smooth, shiny, and dark colored; caruncle usually large and colored, usually red.

DISTRIBUTION.—Approximately 30 species in the Neotropics; three species collected in the Guianas.

LITERATURE.—Pax and Hoffmann (1919c).

Key to the Species of *Pera*

1. Leaf glabrescent, often with scattered simple hairs on petiole and on blade undersurface near base; stamens mostly fused into staminal column 1.5–2.5 mm long; involucre bract subtended by a single bracteole . . . . . *P. distichophylla*\*  
Leaf blade undersurface and petiole with lepidote or stellate hairs; stamens free or only partly fused into staminal column less than 1 mm long; involucre bract subtended by 2 bracteoles . . . . . 2
2. Leaf blade very densely covered with hairs below, blade surface not visible between hairs; filaments slender, longer than 2 mm . . . . . 3  
Leaf blade sparsely to moderately densely covered with hairs below, blade surface clearly visible between hairs; filaments stout, shorter than 2 mm . . . . . 4
3. Hairs lepidote; leaf blade undersurface and capsule densely covered with flat scale-like hairs . . . . . 2. *P. decipiens*  
Hairs stellate; leaf blade undersurface and capsule appearing densely tomentose . . . . . *P. tomentosa*\*\*
4. Capsule glabrous, green or bluish green; ovary glabrous or covered with flat lepidote hairs; leaf blade undersurface and petiole sparsely lepidote, hairs distinctly scale-like often with an uneven or irregularly fringed margin . . . 3. *P. glabrata*  
Capsule and ovary very densely covered with stellate hairs and appearing tomentose, yellowish brown in dried state; leaf blade undersurface and petiole sparsely to moderately densely stellate-lepidote, hairs with long radiating arms . . . . . 1. *P. bicolor*

\*Although *Pera distichophylla* (Mart.) Baill. and *P. tomentosa* (Benth.) Muell. Arg. have been recorded for the Guianas, neither apparently occur there. Both species are found in the neighboring area of Venezuelan Guayana, primarily in the state of Amazonas. The record of *P. distichophylla* in Guyana is based on the collection *Schomburgk 918*, which appears to be mistakenly labelled "British Guiana." The collection is most likely from Amazonas, Venezuela, where Schomburgk also collected extensively.

\*\**Pera tomentosa* originally was based on two discordant types, *Schomburgk 114* from Guyana and *Spruce* from "Capoeiras, Barra do Rio Negro" (Amazonas, Brazil). To resolve this problem the taxon recently was lectotypified by the Spruce collection, thus excluding *Schomburgk 114*, the type of *P. bicolor* (Gillespie, 1993a). This provides a valid and appropriate name, *P. tomentosa*, for this distinct Amazonian species having a densely stellate-tomentose leaf undersurface. This species has not been collected in the Guianas.

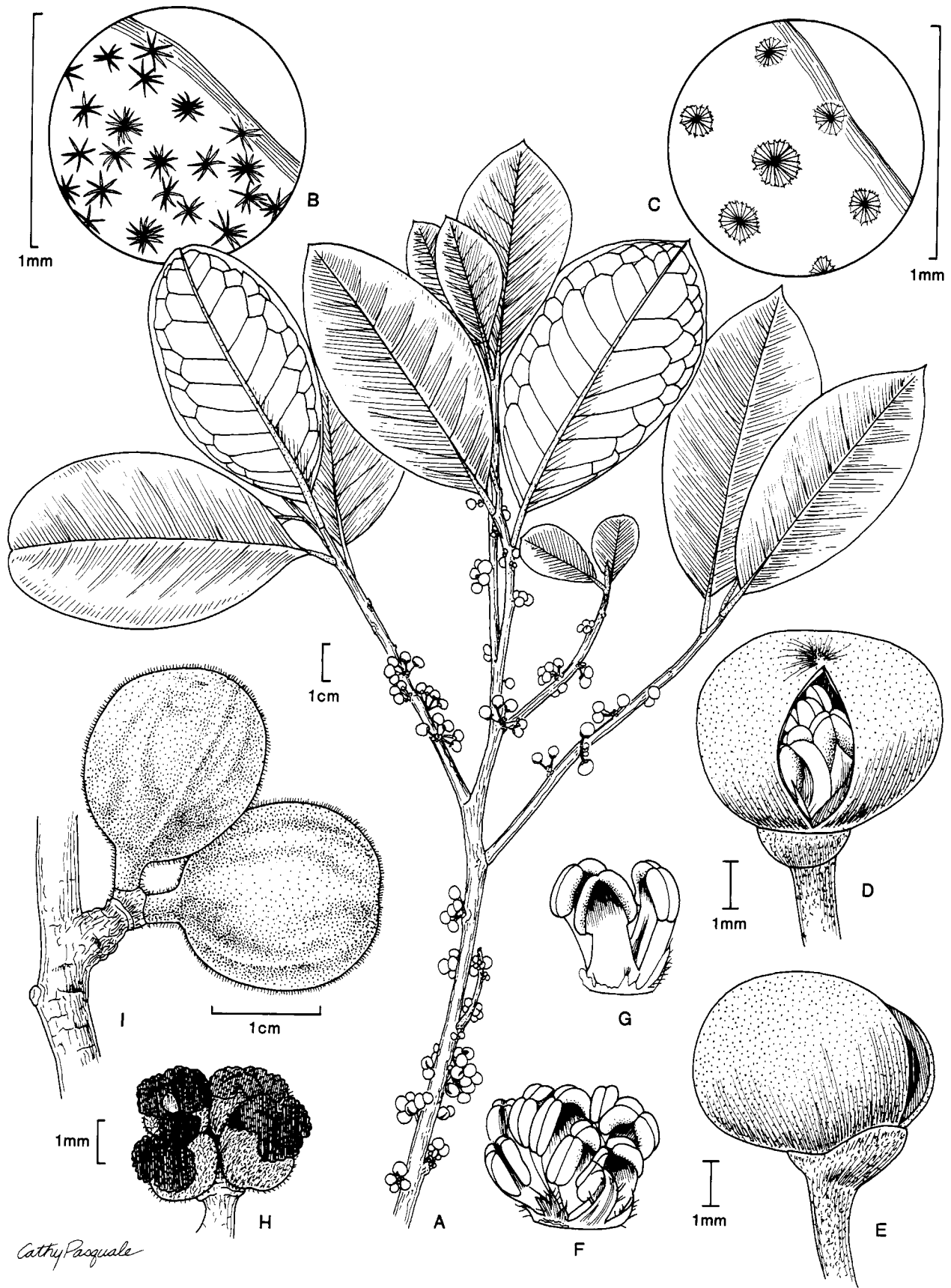
1. *Pera bicolor* (Klotzsch) Muell. Arg.

FIGURE 2A,B,D-I

*Pera bicolor* (Klotzsch) Muell. Arg. in DC., Prodr., 15(2):1028, 1866.  
*Peridium bicolor* Klotzsch, London J. Bot., 2:44, 1843. [Type: Guyana, *Schomburgk 114* (lectotype, G-DC!, designated by Gillespie, 1993a; isotypes, G-2 sheets!, W photo F32519!, K-2 sheets!, P-2 sheets!).]  
*Pera schomburgkiana* Muell. Arg. in DC., Prodr., 15(2):1027, 1866. [Syntypes: Guyana/Venezuela, Roraima, *Ri. Schomburgk 901* (not seen), *905* (syntype, B, destroyed, photo F5376!); *Ro. Schomburgk II 580* (syntype, G-DC!; isosyntypes, G-2 sheets!, P-2 sheets!).]

DESCRIPTION.—Shrub or tree to 33 m, dioecious; indumentum stellate or stellate-lepidote, hairs less than 0.2 mm in diameter, with slender radiating arms. Young stems densely stellate-lepidote. Petiole 0.3–1.3 cm long, densely stellate-lepidote; blade subcoriaceous, obovate or elliptic, 5–11 × 3–6 cm, shiny dark or bright green above, pale grayish green below, drying blackish above and pale tan below, apex rounded or less

often emarginate, short-acuminate or obtuse, base obtuse or acute, glabrous above and often with stellate-lepidote midrib, sparsely covered with stellate-lepidote hairs below. Inflorescence peduncle 1.5–4.5 mm long; involucre bract yellow, subglobose, 4–6 mm in diameter, densely stellate-lepidote, bibracteolate at base. Staminate flowers 3 per involucre bract; calyx irregularly lacinate, to 1.3 mm long or less; stamens (3–) 4; filaments 1–2 mm long, stout, connate at base; anthers ~1 mm long. Pistillate flowers 3 per involucre bract; ovary subglobose, indistinctly 3-lobed, ~2 mm in diameter, very densely tomentose; stigmas obtriangular or obovate, connate at base into a deeply 3-lobed structure, 2–3 mm in diameter. Infructescence peduncle 0.3–0.4 mm long; pedicel 0.3–0.5 mm long; capsule ellipsoid-globose, 15–19 × 14–16 mm, yellow-brown, very densely stellate appearing densely tomentose. Seeds ovoid, radially compressed, black, ~7 × 5–6 × 3 mm; caruncle red, covering about two-thirds of seed.



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FIGURE 2 (left).—*Pera bicolor* (Klotzsch) Muell. Arg. and *Pera glabrata* (Schott) Baill. A,B,D-I, *P. bicolor*: A, habit, flowering branch showing fasciculate staminate pseudanthia; B, leaf blade abaxial surface showing stellate-lepidote hairs; D, staminate pseudanthium at anthesis, ventral view showing slit-like opening of subglobose involucrel bract with staminate flowers inside; E, staminate pseudanthium at anthesis, side view; F, staminate pseudanthium with involucrel bract removed showing cluster of three staminate flowers; G, staminate flower; H, pistillate pseudanthium with involucrel bract removed showing cluster of four pistillate flowers; I, cluster of two capsules on branch (A,B,D-G based on Gillespie 4300, US; H based on Huber 5170, US; I based on Pinkus 194, US); C, *P. glabrata*, leaf blade abaxial surface showing lepidote hairs (based on Pipoly & Godfrey 7371, US).

**DISTRIBUTION.**—Venezuela (Amazonas, Bolívar), the Guianas, and Brazil (Amazonas); 38 collections studied, of which 26 are from the Guianas (G:20, S:3, FG:3).

**ECOLOGY.**—Occurs in savanna, savanna/forest edge, or seasonal forest (e.g., Wallaba forest in Guyana), on white sand or sandy soils, near sea level to 650 m. Flowers have been reported from September to November, fruits from February to April in the Guianas. Trees have been observed to mass flower; small bees were seen visiting and collecting pollen from the very fragrant, lemon-scented, yellow pseudanthia of staminate trees (Gillespie, pers. obs. in Guyana).

**SELECTED SPECIMENS EXAMINED.**—Guyana: Kataima Mazaruni River, Maguire & Fanshawe 32639 (NY, US); mouth of Kako River, upper Mazaruni, Pinkus 194 (GH, MO, NY, US); Moraballi Creek near Bartica, Sandwith 425 (G, NY, P, US). Surinam: Para District, Sectie O, BW 4785 (A, GH, NY, US); Jodensavanne-Mapane Kreek area, Lindeman 4922 (NY). French Guiana: La Mana, 1857, Sagot s.n. (G-DC, P); Route de Charvein-Acarouany, km 6, Serv. For. 311M (NY).

**VERNACULAR NAMES.**—Guyana: Hachiballi (Arawak), Urr (Wapisiana). Surinam: Hachiballi, hatsiballi (Arawak), peprehoedoe (Surinamese), pirikraipjo (Carib). French Guiana: Baaka tiki (Paramaka).

**NOTES.**—There has been much confusion in the literature over the identity of *P. bicolor*, with the name frequently misapplied. The confusion appears to begin with Benth (1854) who grouped three species under *Peridium bicolor*. In his description of *P. bicolor* var. *tomentosum*, he cited both the type collection of *P. bicolor* from Guyana and a collection of a second species from Brazil, now known as *P. tomentosa*. A third species was treated as variety *nitidum* (= *P. decipiens*). Mueller (1865, 1866) treated *P. bicolor* (including var. *nitidum*) and *P. tomentosa* as two distinct species and described two additional species, *P. decipiens* and *P. schomburgkiana* (= *P. bicolor*). Pax and Hoffmann (1919c) treated *P. bicolor* in the sense of variety *nitidum* (including *P. decipiens*) and considered both *P. schomburgkiana* and *P. tomentosa* as distinct species. More recently, in their treatments of Guianan Euphorbiaceae, Lanjouw (1931) and Lemée (1952) treated *P. bicolor* in the correct sense; in addition, Lanjouw noted that *Peridium bicolor* var. *tomentosum* was based on two discordant types (discussed above) and that *Peridium bicolor* var. *nitidum* belongs under *P. decipiens*.

Intraspecific variation in the density of stellate hairs on the leaf blade undersurface may be responsible for some of the confusion described above. The type specimens of *P. schomburgkiana* have a sparsely stellate leaf blade undersurface, whereas the type specimen of *P. bicolor* has a more densely stellate undersurface. They represent opposite ends of a gradation in hair density in this species.

## 2. *Pera decipiens* (Muell. Arg.) Muell. Arg.

FIGURE 3

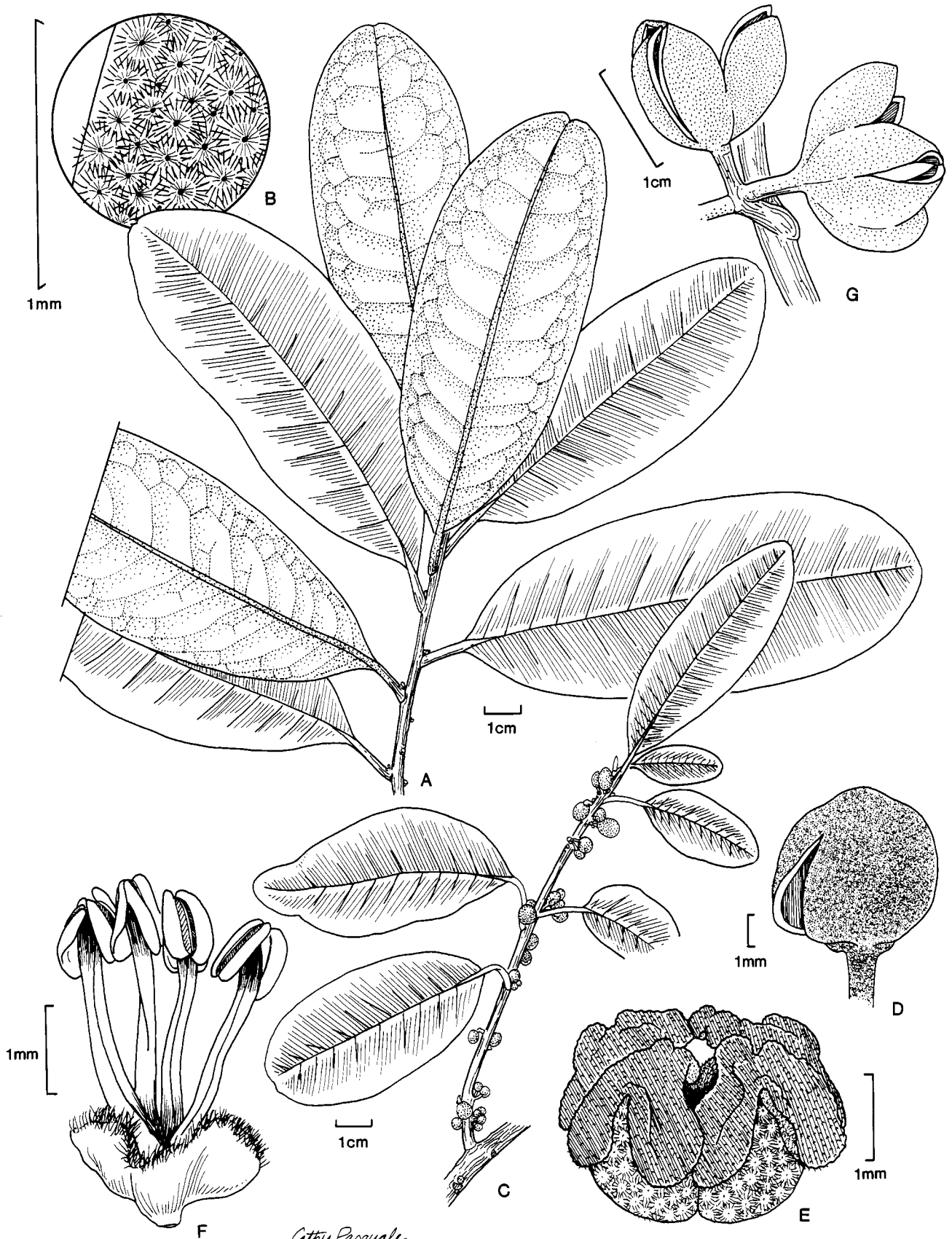
*Pera decipiens* (Muell. Arg.) Muell. Arg. in DC., Prodr., 15(2):1029, 1866.  
*Peridium decipiens* Muell. Arg., Linnaea, 34:201, 1865 [based on type of *Peridium bicolor* var. *nitida*].  
*Peridium bicolor* var. *nitidum* Benth., Hooker's J. Bot. Kew Gard. Misc., 6:323, 1854. [Type: Guyana. Ri. Schomburgk 1070 (lectotype, K!, designated by Gillespie, 1993a; isolectotype, G-fragment!).]  
*Pera nitida* (Benth.) Jabl., Mem. New York Bot. Gard., 17:148, 1967.

**DESCRIPTION.**—Shrub or tree to 30 m; dioecious; indumentum lepidote, hairs ~0.2 mm in diameter, scale-like with darker center and fringed margin. Young stems very densely covered with lepidote hairs. Petiole 0.6–1.8 cm long, very densely lepidote, with adaxial groove; blade subcoriaceous, narrowly elliptic or elliptic, 6–14 × 3–6 cm, dark green above, dull yellow or pale green below, apex obtuse, acute, or sometimes rounded, base obtuse or acute, glabrous with lepidote midrib above, very densely lepidote below. Inflorescence peduncle 3–8 mm long; involucrel bract cream white or pale yellow usually becoming pink, globose, 6–8 mm in diameter, densely lepidote, bibracteolate at base. Staminate flowers 3 per involucrel bract; calyx 1–1.5 mm long, irregularly and shallowly lobed, sparsely to densely covered with stellate or stellate-lepidote hairs, or hairs restricted to margin; stamens 2–4; filaments 2.2–3 mm long, slender, connate at base; anthers 0.7–1 mm long, sagitate. Pistillate flowers 3–4 per involucrel bract; 1–5 rudimentary staminate calyces often present between pistillate flowers; ovary ellipsoid, 2–2.5 × ~1.5 mm, 3-angled, very densely lepidote; stigmas connate into a triangular, peltate structure, 2–3 mm wide. Infructescence peduncle 5–6 mm long, pedicel 5–6 mm long; capsule subglobose, 1.0–1.3 cm in diameter, green, very densely lepidote. Seeds ovoid, radially compressed, dark brown, ~6 × 5 × 2.5 mm, almost covered by flap-like extension of caruncle.

**DISTRIBUTION.**—Venezuela (Amazonas, Bolívar), Guyana, Surinam, Brazil (Amazonas, Pará, Rondônia); 29 collections examined, of which 10 are from the Guianas (G:7, S:3).

**ECOLOGY.**—Occurs in seasonal to moist forest, gallery forest, savanna, or blackwater inundated forest on sandy soils, near sea level to 400 m. Flowering specimens have been collected between September and December in the Guianas. The creamy white or pale yellow pseudanthia are reported to be fragrant.

**SPECIMENS EXAMINED.**—Guyana: Parabara Savanna, Guppy 627 = FD 7642 (FDG, NY, P); Kamoia R., Toucan Mt., Jansen



*Cathy Pasquale*



FIGURE 3 (left).—*Pera decipiens* (Muell. Arg.) Muell. Arg.: A, vegetative branch; B, leaf blade, abaxial surface showing dense covering of lepidote hairs; C, flowering branch, showing fasciculate clusters of pistillate pseudanthia; D, pistillate pseudanthium at anthesis; E, pistillate pseudanthium with involucre bract removed showing cluster of four pistillate flowers; F, staminate flower; G, cluster of two dehiscent capsules (A,B,F based on *Smith 2658*, US; C-E based on *Guppy 267 = FD 7642*, MO; G based on *Berry 604*, MO).

*Jacobs et al. 1751* (P); "British Guiana," 1842, *Ri. Schomburgk 1071* (K); Roraima, *Ro. Schomburgk 685* (G, K, P), 686 (G, G-BOIS, G-DC, K, P); Essequibo River, near mouth of Onoro Creek, *Smith 2658* (A, NY, P, US). Surinam: margin of Kayser Airstrip, Zuid River, 45 km above confluence with Lucie River, *Irwin et al. 57504* (K, MO, NY, US); N slope of '4-Geboiders' Mts., Sipaliwini savanna area, *Oldenburger et al. 264* (K, NY); N of '4-Geboiders' Mts., Sipaliwini savanna area, *Oldenburger et al. 318* (NY).

VERNACULAR NAMES.—Surinam: Pephroedoe.

### 3. *Pera glabrata* (Schott) Baill.

FIGURE 2C

*Pera glabrata* (Schott) Baill., *Étude Euphorb.*, 434, 1858.

*Peridium glabratum* Schott in Spreng., *Syst. veg.*, 4(2)(curae post.):410, 1827.

[Type: none designated (presumably described from one or more specimens in Schott's own collection; Mueller apparently saw these specimens and cited them as *Schott* (1866:1030) and later as *Schott 4318*, 4517 (1874:430).]

*Peridium ferrugineum* Schott in Spreng., *Syst. veg.*, 4(2)(curae post.):410, 1827. [Type: none designated].

*Pera ferruginea* (Schott) Muell. Arg. in DC., *Prodr.*, 15(2):1031, 1866.

DESCRIPTION.—Shrub or tree to 37 m, dioecious; indumentum lepidote, hairs 0.2–0.4 mm in diameter, scale-like with uneven and sometimes irregularly dissected or fringed margin. Young stems sparsely to moderately lepidote. Petiole 0.5–1.2 cm long, sparsely to moderately lepidote; blade chartaceous to subcoriaceous, elliptic, 5–12 × 2.5–5.5 cm, shiny dark green above, dull pale green below, apex obtuse, broadly acute or broadly acuminate, base obtuse or rounded, glabrous above sometimes with sparsely lepidote midrib base, sparsely lepidote below. Inflorescence peduncle 3–7 mm long; involucre bract pale yellow or creamy white, ellipsoid or subglobose, 3–6 mm in diameter, lepidote, bibracteolate at base. Staminate flowers 3 per involucre bract; calyx absent; stamens (3–)4; filaments 0.5–1 mm long, stout, connate at base; anthers 1–1.5 mm long. Pistillate flowers (3–)4 per involucre bract; ovary ellipsoid, ~1.5 × 1 mm, covered with lepidote and sometimes stellate-lepidote hairs or rarely glabrous; stigmas connate into a 3-lobed peltate structure, ~1 mm wide, distinctly verrucose-papillate. Infructescence peduncle 6–12 mm long, pedicel 3–5 mm long; capsule broadly ellipsoid, 8–13 × 7–11 mm, blue-green or pale green, glabrous, smooth, becoming reticulate-wrinkled when mature. Seeds ovoid, radially compressed, black, 4–6 × 3–4.5 × 2–3.5 mm, apex distinctly narrowed; caruncle orange or red, mostly covering adaxial seed surface.

DISTRIBUTION.—Venezuela, the Guianas, Brazil (Amazonas, Pará, eastern and southeastern Brazil); 63 collections studied, of which 25 are from the Guianas (G:17, S:2, FG:6).

ECOLOGY.—Occurs in seasonal lowland to montane forest, often on white sand, sea level to 700 m in the Guianas, to 1400 m in Venezuela. Flowers have been reported in March, April, September, and November, fruit in May and November in the Guianas. The pale yellow or creamy white pseudanthia are reported to be fragrant.

SELECTED SPECIMENS EXAMINED.—Guyana: Mazaruni Station, *FD 5409* (K, US); Mainstay Village, 7°15'N, 58°32'W, *Gillespie & Persaud 1058* (US); Linden-Soesdyke Hwy., between Dora and Maibia Creek, 6°18'N, 58°14'W, *Pipoly et al. 9705* (NY, US); Basin of Rupununi R., Isherton, *Smith 2418* (G, US). Surinam: Kaboerie, *BW 4847* (A, GH, K, US); Zanderij I., *Stahel 273* (A, GH, K). French Guiana: Commune de Iracoubo, 5°28'N, 53°14'W, *Cremers 9627* (US); Ile de Cayenne, route de Rochambeau, *Oldeman BC9* (MO, NY, US).

VERNACULAR NAMES.—Guyana: Hatchi-balli (Arawak), kamua-tan (Wapisiana). Surinam: hatsiballi koelnoe.

### Tribe PLUKENETIEAE

Tribe Plukenetieae (Benth.) Hutch., is a cohesive group of 14 genera distributed worldwide in tropical and warm temperate regions. The tribe may be distinguished by its bisexual, racemose or spicate inflorescences (unisexual in *Acidoton* Sw. and some African *Tragia* spp.), and entire styles that are basally to completely connate and often massive (most other members of the Acalyphoideae core group have unisexual inflorescences and styles that are typically branched and/or free). In addition, many species have a scandent habit and/or urticating hairs, both unusual features in the Euphorbiaceae.

Tribe Plukenetieae comprises three subtribes, the Dalechampiinae, Plukenetiinae, and Tragiinae (Webster, 1994). The Tragiinae have urticating hairs, a trilocular ovary, and lack laminar glands, whereas the Plukenetiinae lack urticating hairs and have a 3- or 4-locular ovary and usually laminar glands on the leaf blade. Pollen of the Plukenetiinae is uniformly tricolpate, whereas that of the Tragiinae varies from tricolpate to weakly aperturate and inaperturate (Gillespie, 1994a). Tragiinae genera known from the Guayana Region include *Acidoton* and *Tragia*, whereas genera of Plukenetiinae known from this region include *Astrococcus* Benth., *Haematostemon*, and *Plukenetia* (Gillespie, 1993a). Of these genera, only *Haematostemon*, *Plukenetia*, and *Tragia* have been collected from the Guianas. *Acidoton* may perhaps be expected to occur in the Guianas, having been collected from the neighboring state of Bolívar, Venezuela, and is therefore included in the key. *Astrococcus*, on the other hand, is endemic to blackwater inundated forest in the upper Rio Negro region and is unlikely to be found in the Guianas.

The third subtribe, Dalechampiinae, comprising the single

genus *Dalechampia*, is unique in the Euphorbiaceae in having 2-bracted, bisexual pseudanthia. The subtribe, previously considered a distinct but related tribe (Webster, 1975), has recently been placed in tribe Plukenetieae (Webster, 1994). The presence of urticating hairs, styles that are completely connate into a thickened, often massive column, bisexual inflorescences, and a usually scandent habit strongly suggest a close affinity with other members of tribe Plukenetieae.

**3. Genus *Dalechampia* L.**

*Dalechampia* L. Sp. Pl., 1054, 1753; Gen. Pl., ed. 5:473, 1754. [Type: *Dalechampia scandens* L.]  
*Megalostylis* Spencer Moore, J. Bot., 54:208, 1916. [Type: *Megalostylis poeppigii* Spencer Moore.]

DESCRIPTION.—Perennial vines or shrubs, monoecious; latex absent. Stems climbing, spreading, or erect, usually covered with urticating hairs. Leaves simple or compound, alternate, petiolate, stipulate, with pair of stipels at base of blade (stipels sometimes obscure or deciduous); blade pinnately or palmately veined, margin entire to deeply lobed; distinct petiolar and laminar glands absent. Inflorescence pseudanthial, subtended by 2 usually large, showy bracts,

comprising a cymule of 3 pistillate flowers and 3–5-branched pleiochasium of 4–(~15) staminate flowers; pistillate cymule subtended by an involucl of 1 bract and 0–2 bractlets; staminate pleiochasium subtended by a cup-like involucellar bract, a bilabiate involucl, or 4(–5) free bracts. Staminate flowers with calyx splitting into 3–6 valvate segments at anthesis; corolla and disc absent; stamens 5–90 on flat, dome-shaped, or elongated receptacle (column); anthers sessile or on short filaments, usually in cluster at apex of column, dehiscent longitudinally. Pistillate flowers with 5–12 entire or lobed sepals; petals and disc absent; ovary 3-locular; styles connate into elongated column, often dilated at apex. Fruit 3-seeded capsule, dehiscent explosively by elastic twisting of dry, more or less woody cocci. Seeds subglobose to globose, ecarunculate, surface smooth, roughened, or tuberculate, usually gray-brown mottled.

DISTRIBUTION.—Approximately 120 species, ~95 in neotropics, 10 in Africa, 10 in Madagascar, and six in Asia; 16 species collected in the Guianas, with two additional species from neighboring Venezuelan Guayana likely to occur in the Guianas.

LITERATURE.—Pax and Hoffmann (1919b); Webster and Armbruster (1991).

**Key to the Species of *Dalechampia***

1. Shrubs; leaves pinnately veined; involucral bracts pink (rarely yellowish) at anthesis; inflorescence glands yellow or greenish, surface papillate, producing spicy fragrance . . . . . 8. *D. magnoliifolia*  
 Vines; leaves palmately veined; involucral bracts white, green, or pink at anthesis; inflorescence glands, when present, variously colored, usually producing resin . . . . . 2
2. Leaves compound, 3-foliolate or rarely 4- or 5-foliolate; involucral bracts conspicuous, green at anthesis . . . . . 3  
 Leaves simple; involucral bracts inconspicuous or conspicuous, white, pink, or green at anthesis . . . . . 5
3. Involucral bracts spatulate, 5–8 mm long, 3–4 mm wide, deciduous prior to fruiting; staminate involucellar bracts free, 4 in number; surface of stigmas papillate . . . . . 12. *D. papillistigma*  
 Involucral bracts broadly ovate, 10–15 mm long, 10–15 mm wide, persistent in fruit; staminate involucellar bracts connate or bilabiate; surface of stigmas smooth . . . . . 4
4. Pistillate sepals shallowly to deeply lobed, rachis broad, width >1/4 length, fringed with dense pubescence . . . . . 18. *D. aff. triphylla*  
 Pistillate sepals pinnatifid, rachis narrow, width <1/4 length, hispid . . . . . 17. *D. aff. cissifolia*
5. Leaves unlobed; involucral bracts subequal, inconspicuous, small (<6 mm long), stipuliform, green at anthesis, or dimorphic (one small, the other conspicuous, >1 cm long, whitish); inflorescence gland usually absent; pistillate sepals 6, unlobed . . . . . 6  
 Leaves lobed or unlobed; involucral bracts subequal, conspicuous, ≥1 cm in length; resin-producing inflorescence gland present (vestigial and inconspicuous in *D. brownbergensis*); pistillate sepals 6–12, lobed or unlobed . . . . . 12

- 6. Leaves narrow, width  $< \frac{1}{3}$  length, with arcuate secondary veins branching from basal and distal regions of the central vein, base of blade obtuse and rounded; staminal column extremely short or obsolete; stylar column cylindrical, slightly dilated at extreme tip . . . . . 3. *D. brevicolumna*  
 Leaves wide, width  $> \frac{1}{3}$  length, with 1-3 arcuate secondary veins attached to the central vein only in its distal  $\frac{1}{2}$ , base of blade truncate to cordate; staminal column well developed, conspicuous; stylar column enlarged, more or less clavate, not dilated at extreme tip . . . . . 7
- 7. Stems, petioles, leaves, and peduncles densely hirsute-lanate with orange hairs; pseudanthia sessile, usually 2 or more in leaf axils . . . . . 11. *D. olympiana*  
 Stems, petioles, leaves, and peduncles glabrescent to hirsute, but hairs not orange; pseudanthia borne on peduncles (short shoots)  $> 1$  cm long, usually solitary in leaf axils . . . . . 8
- 8. Base of leaf blades truncate to shallowly cordate; stipules ovate, 5 mm long, early deciduous; fertile arms in staminate pleiochasium 4; staminate flowers 12-13; stigma extending from tip to  $> \frac{3}{4}$  length of style . . . . . 9  
 Base of leaf blades shallowly to deeply cordate (or hastate in immature plants); stipules lance-ovate to lanceolate, usually  $> 5$  mm long (except *D. parvibracteata*), deciduous only after leaves have expanded, or persistent; fertile arms in staminate pleiochasium 3-4; staminate flowers 10-13; stigma extends from tip to  $< \frac{3}{4}$  length of style or if to  $> \frac{3}{4}$  length, then widest part of stylar column  $< \frac{1}{2}$  distance from base; pistillate sepals persistent into fruit . . . . . 10
- 9. Stylar column curved upwards toward staminate cymule, width  $\sim \frac{1}{5}$  length, tip markedly foveolate; base of leaves usually truncate, stipules deciduous prior to full expansion of leaves . . . . . 10. *D. micrantha*  
 Stylar column more or less straight, very thick, width  $\sim \frac{1}{3}$  length, tip not markedly foveolate; base of leaves usually shallowly cordate, stipules deciduous usually after expansion of leaves . . . . . 6. *D. fragrans*
- 10. Stylar column broadest at  $\frac{1}{3}$  to  $\frac{1}{2}$  length from base, tapering to blunt, attenuate tip; smooth stigmatic surface extending from tip to  $\frac{2}{3}$  to  $\frac{3}{4}$  length of stylar column, not contrasting markedly with stylar base; sinus at base of leaves usually deltoid, narrow at attachment of blade to petiole . . . . . 2. *D. attenuistylus*  
 Stylar column clavate, broadest at  $\sim \frac{2}{3}$  to  $\frac{3}{4}$  its length from base; smooth stigmatic surface extending from tip to  $\frac{1}{4}$  to  $\frac{2}{3}$  length of stylar column, contrasting markedly with pubescent stylar base; sinus at base of leaves usually broad and U-shaped . . . . . 11
- 11. Involucral bracts usually dimorphic, the one subtending pistillate flowers  $> 1$  cm long, whitish, the one subtending staminate flower  $< 5$  mm long, stipuliform, green; stigmatic surface extending from tip to  $\sim \frac{2}{3}$  length of stylar column . . . . . 7. *D. heterobracteata*  
 Involucral bracts subequal,  $< 5$  mm long, stipuliform, green; stigmatic surface extending from tip to  $\sim \frac{1}{4}$  length of stylar column . . . . . 13. *D. parvibracteata*
- 12. Leaves always unlobed . . . . . 13  
 Leaves all 3-lobed or both unlobed and 3-lobed present on same plant (except very young plants, which may have only unlobed leaves) . . . . . 16
- 13. Staminate pleiochasium with 4 free involucellar bracts; inflorescence gland comprising concentrically arranged bractlets with lacinate margins, secreting greenish or brownish resin; involucral bracts linear and green or ovate and pink . . . . . 14  
 Staminate pleiochasium with involucel of bracts fused for at least basal  $\frac{1}{3}$  or forming a bilabiate cup; inflorescence gland of more or less laminar bractlets with entire or minutely fimbriate margins, secreting clearish or yellowish resin; involucral bracts broadly ovate, pale green or white . . . . . 15

14. Leaf blades 7–27 cm long with brownish pubescence below, involucre bracts green at anthesis, 1–2 cm long, inflorescence gland secreting bluish green resin, style more or less evenly columnar, pistillate sepals 6, unlobed, fruit 3.5–4 cm in diameter . . . . . 9. *D. megacarpa*  
 Leaf blades 5–15 cm long, lacking brownish pubescence, involucre bracts pale pink with reddish veins, 3–5 cm long, inflorescence gland secreting brownish maroon resin, style with distinct peltate stigmatic tip, pistillate sepals 6–12, twice-pinnatifid, fruit <2 cm in diameter . . . . . 5. *D. dioscoreifolia*
15. Involucre bracts white at anthesis, >3 cm long, entire or shallowly 3-lobed, with 7–9 prominent veins; inflorescence gland secreting yellowish resin; tips of styles broadly dilated and symmetrically peltate . . . . . 1. *D. affinis*  
 Involucre bracts pale green to whitish at anthesis, <3.5 cm long, deeply 3-lobed to ~<sup>1</sup>/<sub>2</sub> their length, with 5 prominent veins; inflorescence gland secreting clear to whitish resin; tips of styles modestly and asymmetrically dilated . . . . .  
 . . . . . 14a. *D. scandens* var. *scandens*
16. Margins of leaf stipules, involucre bracts, and (usually) leaf blades capitate glandular, glandular appendages secreting sticky resin . . . . . 15. *D. stipulacea*  
 Margins of leaf stipules, involucre bracts, and leaf blades subentire to irregularly dentate, but without glandular appendages that secrete sticky resin . . . . . 17
17. Leaf stipules ovate to lance-ovate, persistent; involucre bracts 3-lobed to ~<sup>1</sup>/<sub>2</sub> their length, <3.5 cm long at anthesis, with 5 prominent veins; inflorescence gland secreting clear to whitish resin . . . . . 18  
 Leaf stipules lance-ovate to lance-linear, deciduous; involucre bracts shallowly 3-dentate at apex, >3 cm long at anthesis, with 7–9 prominent veins; inflorescence gland inconspicuous or secreting yellowish resin . . . . . 19
18. Young stems and petioles with sparse to moderately dense spreading straw-colored pubescence; underside of mature leaves glabrescent to strigulose; involucre bracts pale green to whitish, margins with small fimbria, these at most weakly capitate, <0.5 mm long; margin of proximal bract of pistillate involucre entire; stylar column with slightly and asymmetrically dilated tip . . . . .  
 . . . . . 14a. *D. scandens* var. *scandens*  
 Young stems and petioles with very dense spreading orange pubescence; underside of mature leaves lanate; involucre bracts white, margins with strongly capitate tentacular processes, generally 1–1.5 mm long; margins of proximal bract of pistillate involucre capitate glandular; stylar column with broadly expanded symmetrically peltate tip . . . . . 14b. *D. scandens* var. *fallax*
19. Leaf stipules lance-linear; involucre bract whitish cream at anthesis; inflorescence gland prominent, secreting yellowish resin . . . . . 16. *D. tiliifolia*  
 Leaf stipules lance-ovate to lanceolate; involucre bracts pale green at anthesis; inflorescence gland inconspicuous and vestigial, not secreting resin . . . . .  
 . . . . . 4. *D. brownsbergensis*

### 1. *Dalechampia affinis* Muell. Arg.

*Dalechampia affinis* Muell. Arg., *Linnaea*, 34:223, 1865. [Type: French Guiana, La Mana, *Sagot s.n.* (lectotype, G, designated by Webster and Armbruster, 1991).]

DESCRIPTION.—Twining or sprawling vine. Leaves simple; stipules lance-linear, 3–7 × ~1 mm; petioles 2–6 cm long; blades chartaceous, usually ovate, rarely lanceolate, always unlobed, 4–12 × 3–9 cm, apex acuminate, base shallowly to deeply cordate, sparsely pubescent above, velutinous below. Inflorescence pseudanthial; the two bracts involucre, cream-

white at anthesis, broadly ovate, tip acuminate, usually entire, 2–5 × 2–4 cm, velutinous, with 7–9 major veins; pseudanthium containing ~10 staminate flowers and 3 pistillate flowers; inflorescence gland secreting yellow resin. Staminate flowers with ~40 stamens. Pistillate flowers with calyx of 10–12 sepals, these pinnatifid, densely hispid; pistil with elongate stylar column, 6–10 mm long, tip symmetrically umbraculiform. Fruit surface sparsely to densely hispid; seeds spherical, mottled brown and gray, ~4 mm in diameter, surface smooth.

DISTRIBUTION.—Widespread in lowland northeastern South

America (eastern Venezuela, Guyana, Surinam, French Guiana, and northern Brazil); 36 collections studied, all from the Guianas (G:10, S:13, FG:13).

ECOLOGY.—Occurs in open woodland and savanna below 500 m. The copious yellow resin secreted by the inflorescence glands is collected in Brazil by female euglossine bees (including *Euglossa*; Apidae) that pollinate flowers in the process (Armbruster and Webster, 1981, 1982). It apparently flowers December through July.

SELECTED SPECIMENS EXAMINED.—Guyana: Naamryck Canal, Essequibo Islands-West Demerara, ~3.5 km SW of Parika, 6°50'N, 58°27'W, *Gillespie & Gopaul 1009* (ALA, US); Rockstone, bank of Essequibo River, *Gleason 880* (NY, US). Surinam: Nickerie, near Kabalebo Dam project, *Lindeman et al. 286* (K, MO, NY, U, US); Zuid River, between Kayser airstrip and confluence with Lucie River, 3°20'N, 56°49'W–3°10'N, 56°29'W, *Maguire et al. 54028* (MO, NY, U, US). French Guiana: Village Eskol, 4°45'N, 52°20'W, *Cremers 9820* (CAY, NY, US); Tampoc River, SE of Maripasoula, *Moretti 698* (CAY).

NOTES.—This species is similar and very closely related to *D. tiliifolia*. From *D. tiliifolia* it differs primarily in having exclusively unlobed leaves, symmetrically peltate style tips, and involucral bracts usually with unlobed tips.

## 2. *Dalechampia attenuistylus* Armbruster

*Dalechampia attenuistylus* Armbruster, Brittonia, 41:44, 1989. [Type: Venezuela, Bolívar, Santa Elena de Uairen, *Armbruster et al. 87-153* (holotype, MO!; isotypes, ALA!, MY!, NY!, VEN!).]

DESCRIPTION.—Twining vine reaching low forest canopy. Leaves simple; stipules lanceolate to ovate, 3–8 × 1–2 mm; petioles 1–4.5 cm long; blades unlobed, 3–10 × 2–7 cm, base cordate with deltoid sinus, sinus usually narrow at attachment of blade to petiole. Pseudanthial inflorescences with inconspicuous stipuliform involucral bracts 3–6 mm long, rarely lower (basal) bract up to 1 cm long, 10(–11) staminate flowers and 3 pistillate flowers per inflorescence. Staminate flower with 8–10(–11) stamens. Pistillate flowers with 6 sepals, these unlobed; stylar column straight, widest at 1/3–1/2 length from base, distally tapered to attenuate, blunt tip; stigma light green, extending from tip to 2/3–3/4 length of stylar column. Fruit with small persistent sepals; seeds subspherical, ~4 mm in diameter, surface nearly smooth.

DISTRIBUTION.—Known only from southeastern Bolívar, Venezuela, and southern Surinam, but likely to occur in Guyana and northern Brazil; three collections studied, one from Surinam.

ECOLOGY.—Vine in forest openings and lower canopy of moist riparian forest, 800–1000 m. In flower and fruit middle to late December.

SPECIMENS EXAMINED.—Surinam: Lely Mountains, *Mori and Bolten 8550* (MO, NY, U, US). Venezuela: Bolívar, Santa

Elena de Juairén, first bridge south of town, *Armbruster et al. 93-01* (ALA).

NOTES.—A member of section *Rhopalostylis*, this species is probably most closely related to *D. parvibracteata*. As is the case for all members of the section, it lacks the prominent inflorescence gland characteristic of most of the rest of genus. It differs from other members of the section in having tapered styles that are widest at about one-third the length and in having 10 staminate flowers arranged in 3 pleiochasial arms in the inflorescence.

## 3. *Dalechampia brevicolumna* Armbruster

FIGURE 4

*Dalechampia brevicolumna* Armbruster, Syst. Bot., 21:232, 1996. [Type: Near St. Elie, French Guiana, *Prevost 661* (holotype, CAY!; isotype, U!).]

DESCRIPTION.—Twining vine reaching canopy. Leaves simple; stipules lanceolate, 2–4 × 0.8–1 mm; petioles 4–20 mm long; blades 5–11 × 2–5 cm, width < 1/3 length, base rounded, triplinerved, secondary veins diverge from central primary vein throughout its length. Pseudanthial inflorescences with inconspicuous stipuliform involucral bracts 2.5–3.0 mm long, 6–9 staminate flowers, 3 pistillate flowers. Staminate flowers with 20–30 stamens attached to more or less flat receptacle, column extremely short or absent. Pistillate flowers with 5–6 sepals, these lanceolate, unlobed; stylar column more or less cylindrical, straight, with slightly dilated tip, stigma extending from tip to > 3/4 length of stylar column.

DISTRIBUTION.—Apparently endemic to French Guiana and Surinam; five collections studied (FG:4, S:1).

ECOLOGY.—Occurs in secondary vegetation and at edge of wet forest. In French Guiana it is pollinated by female resin-collecting anthidiine bees (*Hypanthidium* sp., Megachilidae) and conspecific males landing on the flowers in search of females. This species appears to have peak flowering in late June through August, although flowers also have been collected in March; fruits are present June to October.

SPECIMENS EXAMINED.—French Guiana: Saül-Belizon area, *Oldeman 1472* (CAY); near St. Elie, *Prevost 665* (CAY, U); near St. Elie, *Prevost 1673* (US). Surinam: Tumuc Hamuc Mountains, Talouaken, *Acevedo-Rodriguez et al. 6026* (US).

NOTES.—This is a very unusual species. It is placed in its own section, *Brevicolumnae* (Armbruster, in press). It resembles members of sect *Rhopalostylis* in having small, stipuliform involucral bracts and leaf lamina with sparse pubescence. It differs from members of the section in its leaves having secondary veins distributed along the length of the central primary vein, the arrangement of staminate flowers and involucellar bractlets, and staminate flowers with extremely short staminal columns. It resembles more advanced species in section *Dalechampia* (including *D. scandens* and *D. stipulacea*) in having inflorescence resin glands comprising laminar bractlets with entire margins.

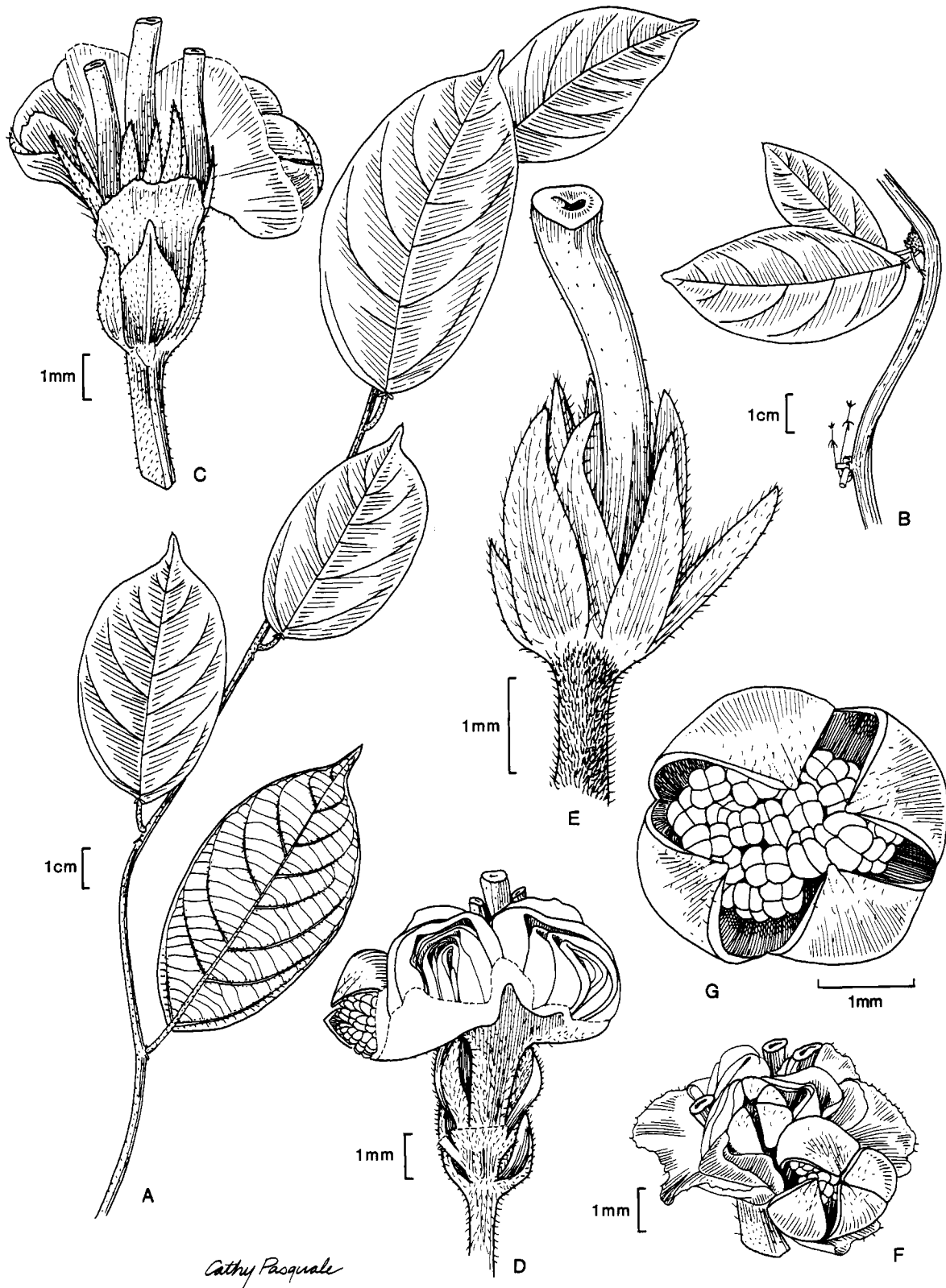


FIGURE 4.—*Dalechampia brevicolumnna* Armbruster: A, habit; B, habit with infructescence in post-dehiscence stage; C, inflorescence, pistillate side; D, inflorescence with resin gland, staminate side with part of involucellar bract removed; E, pistillate flower; F, staminate pleiochasium lacking resin gland, as is occasionally observed; G, staminate flower (based on *Prevost 661*).

#### 4. *Dalechampia brownsbergensis* Webster & Armbruster

FIGURE 5

*Dalechampia brownsbergensis* Webster & Armbruster, Syst. Bot., 7:484, 1982. [Type: Surinam, Brokopondo, Brownsberg Nature Preserve, 4°57'N, 55°11'W, Webster & Armbruster 24124 (holotype, DAV!; isotypes, ALA!, BBS!, GH!, MO!, NY!, U!).]

DESCRIPTION.—Twining vine reaching canopy. Leaves simple; stipules elliptic-lanceolate, 4.5–10 × ~2–3.5 mm; petioles 4.5–13 cm long; blades chartaceous, ovate, usually 3-lobed, 10–22 × 10–25 cm, apex of middle lobe cuspidate, base deeply cordate, glabrescent above, puberulent below. Inflorescence pseudanthial; the two bracts involucreal, pale green at anthesis, broadly ovate, tip shallowly 3-lobed, 2–5 × 2–5 cm, 9–11 veined at base, velutinous; resiniferous gland inconspicuous, vestigial, not secreting resin. Staminate flowers with 5–22 stamens. Pistillate flowers with calyx of 10–12 sepals, these pinnatifid, densely hispid; pistil with elongate stylar column, 7–10 mm long, tip asymmetrically trigonous. Fruit a capsule, surface glabrate, prominently raised-reticulate; seeds spherical, mottled brown and gray, ~3.7 mm in diameter, surface smooth.

DISTRIBUTION.—Occurs in Surinam and eastern Venezuela, also probably Guyana. Five collections studied, two of which are from Surinam.

ECOLOGY.—Occurs in wet forests below 100 m. This species lacks the resiniferous inflorescence gland characteristic of most species. It instead secretes a fragrance from the stigmatic surface of the pistillate flowers and attracts pollinating male euglossine bees that collect the fragrance (Armbruster et al., 1992). Apparently flowers year-round; flowers and fruits are present in July, November, and December.

SPECIMENS EXAMINED.—Surinam: Brokopondo, Brownsberg Nature Park, ~4°55'N, 55°10'W, Armbruster & Herzig 85–102 (ALA).

#### 5. *Dalechampia dioscoreifolia* Poepp.

FIGURE 6

*Dalechampia dioscoreifolia* Poepp., Nov. gen. spec. pl., 3:20, 1841. [Type: Peru, Maynas, Poeppig 2163 (holotype, B, destroyed; lectotype, W, designated by Webster and Armbruster, 1991).]

DESCRIPTION.—Twining vine reaching canopy. Leaves simple; stipules lanceolate, 3.0–3.5 × 1.0–1.5 mm wide; petioles 2–7 cm long; blades chartaceous, ovate, unlobed, 5.5–13.5 × 4.0–9.5 cm, base distinctly cordate, tip acuminate. Pseudanthial inflorescence with showy pink involucreal bracts, these ovate, 1.3–4.5 × 1.2–3.0 cm, with 3–5 major veins, base clawed, usually 10 staminate flowers and 3 pistillate flowers; inflorescence gland secretes brown-maroon resin. Staminate flowers with 20–30 stamens. Pistillate flowers with umbraculiform stylar column, 3–6 mm long, expanded tip symmetrically

peltate-disciform; stigmatic surface confined to the expanded stylar tip. Seeds subspherical and weakly 3-angled, ~5 mm long.

DISTRIBUTION.—Occurs from Nicaragua to Peru; 16 collections studied, eight of which are from French Guiana.

ECOLOGY.—This robust vine grows at the edge of forest or into the canopy of moist to wet primary or secondary forest below 1200 m. In Mesoamerica and Peru it is pollinated by female *Eulaema* spp. and *Euglossa* spp. that collect resin from the inflorescence gland (Armbruster and Herzig, 1984). Flowers present from January through August.

SPECIMENS EXAMINED.—French Guiana: Saül, Beekman 59 (CAY); Saül, route to Belizon, Feuillet 417 (CAY); Grand Inini River, east of Maripasoula, Granville 7292 (B, CAY, MO, P); Saül, Maas et al. 2226 (CAY, U); Crique Ket-oko, NE of Saül, Oldeman 2067 (CAY, MO, NY, P); Saül area, Oldeman B.3227 (CAY, NY, U); Saül, Raynal-Roques 20006 (CAY).

#### 6. *Dalechampia fragrans* Armbruster

*Dalechampia fragrans* Armbruster, Bot. J. Linn. Soc. London, 105:150, 1991. [Type: Surinam, Brokopondo, Brownsberg Nature Park, 4°55'N, 55°10'W, Armbruster & Herzig 85–101 (holotype, MO!; isotypes, ALA!, NY!, UVS!).]

DESCRIPTION.—Twining vine reaching canopy. Leaves simple; stipules ovate, 3–4 × 1–2 mm, usually deciduous prior to full expansion of leaves; petiole 1–5 cm long; blade ovate, unlobed, 6–14 × 4–12 cm, with shallowly cordate base, usually with broad U-shaped sinus. Pseudanthial inflorescences with inconspicuous stipuliform involucreal bracts < 5 mm long, usually 13 staminate flowers, and 3 pistillate flowers. Staminate flowers with 4–5 stamens. Pistillate sepals 6, unlobed; stylar column clavate, straight, widest ~2/3 of the way to the rounded tip, 7–10 mm long, stigma green, extending from tip to ~3/4 length of stylar column.

DISTRIBUTION.—Known from Surinam, French Guiana, and Amapá, Brazil; five collections studied (S:3; FG:1).

ECOLOGY.—Occurs in canopy of, or gaps in, lowland wet forest. Flowers in early to middle November. Members of this species secrete a fragrance from the stigmatic surface of the pistillate flowers, attracting (in Suriname) a number of species of male euglossine bees (Hymenoptera: Apidae), including *Eulaema* spp., *Eufriesea* spp., and *Euglossa* spp. These fragrance-collecting bees pollinate the flowers (Armbruster et al., 1992).

SPECIMENS EXAMINED.—Surinam: Brokopondo, Brownsberg Nature Park, 4°55'N, 55°10'W, Armbruster and Herzig 85–104 (ALA); Brownsberg, Maas et al. 2320 (MO). French Guiana: ~52 km south of Cayenne, Mori et al. 8693 (NY, P).

NOTES.—This species is a member of section *Rhopalosylis* and lacks the prominent resiniferous inflorescence gland characteristic of most members of the genus.

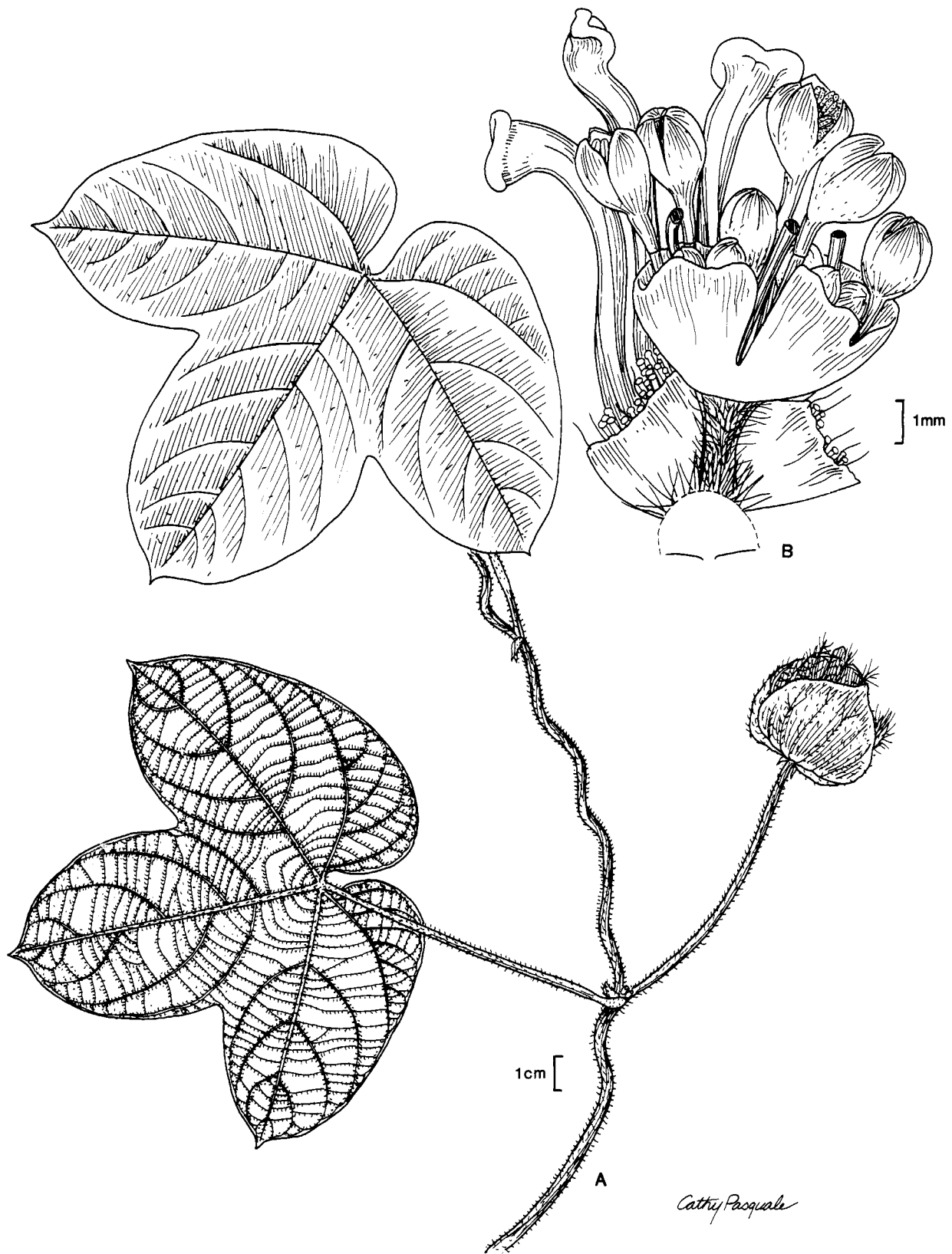


FIGURE 5.—*Dalechampia brownsbergensis* Webster & Armbruster: A, habit with infructescence; B, inflorescence (based on McDowell 4318).



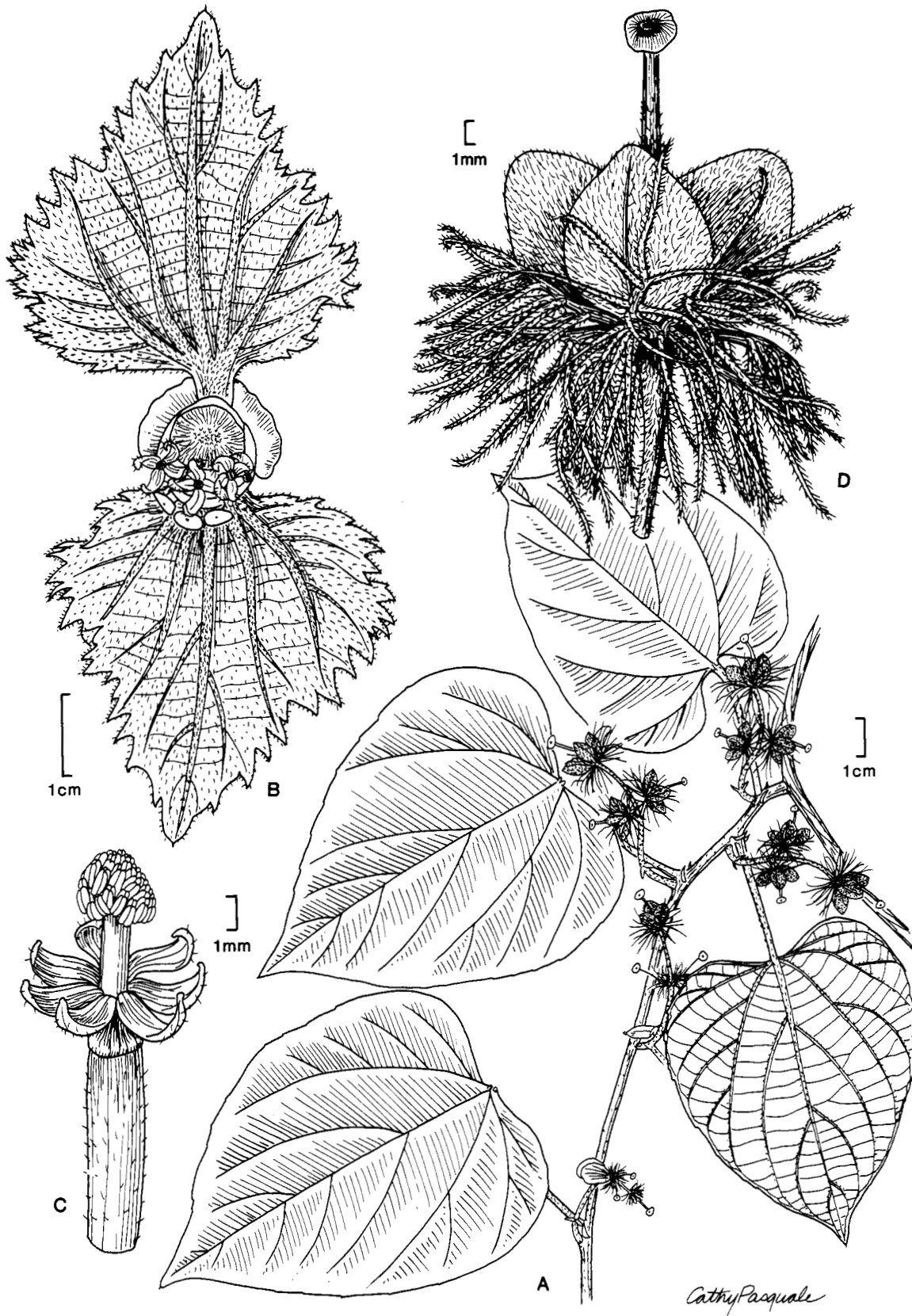


FIGURE 6.—*Dalechampia dioscoreifolia* Poepp.: A, habit; B, inflorescence; C, staminate flower; D, capsule, note persistent style and fimbriate calyx (A,D based on Williams 303; B based on Armbruster & Herzig 79-212; C, based on Bell et al. 93-326).

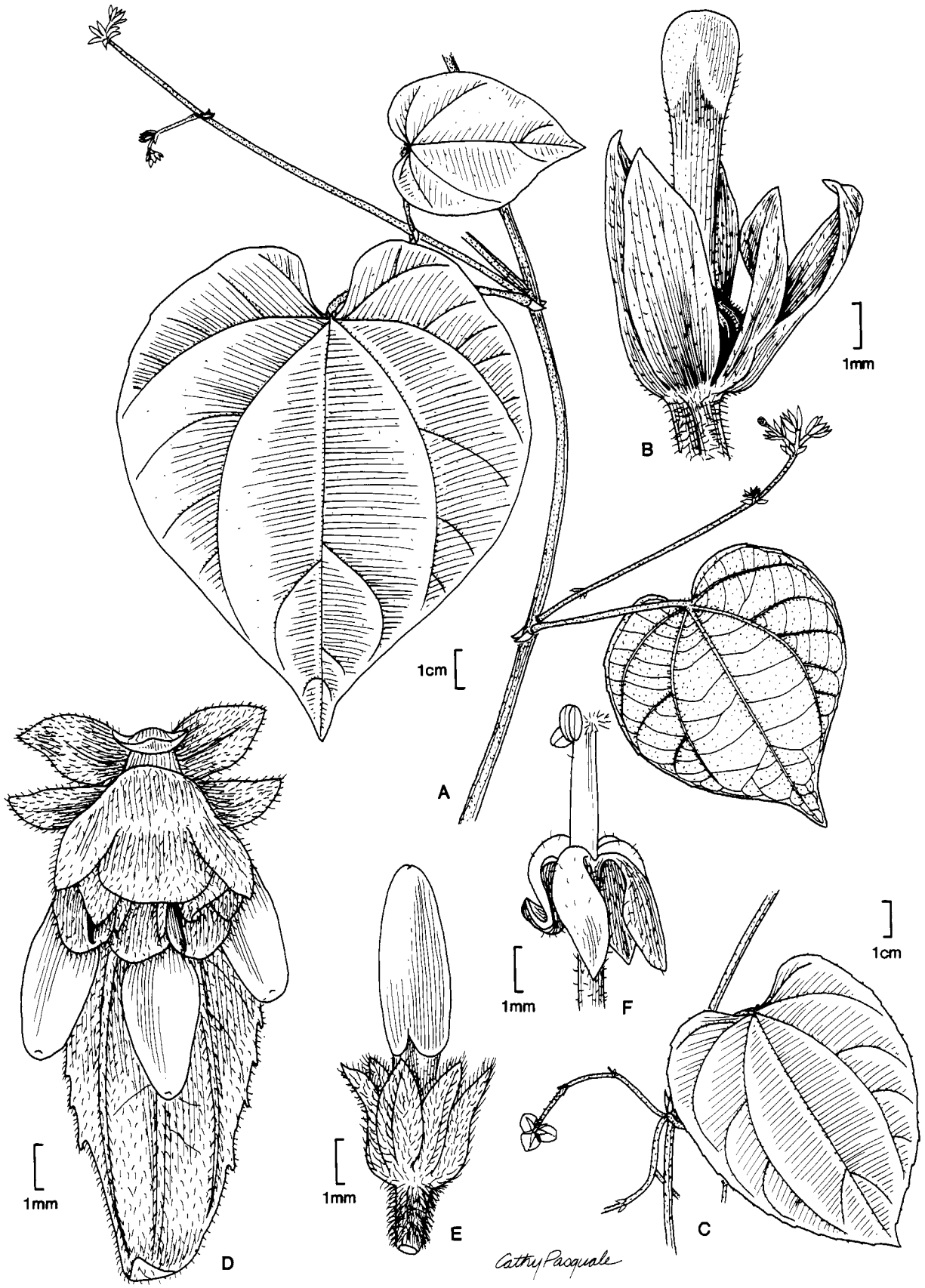


FIGURE 7 (left).—*Dalechampia parvibracteata* Lanj. and *Dalechampia heterobracteata* Armbruster. A,B, *D. parvibracteata*: A, habit; B, pistillate flower (A,B based on McDowell 2264); C-F, *D. heterobracteata*: C, habit; D, inflorescence; E, pistillate flower; F, staminate flower (with all but two anthers removed) (C based on Feuillet 3015; D-F based on Armbruster et al. 87-157).

### 7. *Dalechampia heterobracteata* Armbruster

FIGURE 7C-F

*Dalechampia heterobracteata* Armbruster, Syst. Bot., 21:226, 1996. [Type: Guyana, Mazaruni Station, by Karau Creek, *Sandwith 1565* (holotype, K!; isotypes, BM!, NY!, P!, U!, US!).]

DESCRIPTION.—Twining vine reaching canopy. Leaves simple; stipules lanceolate, (3)5–7 × 1–1.5 mm, persistent; petioles 3–9 cm long; blades 6–19 × 5–15 cm, generally broadest at  $1/4$  to  $1/2$  distance from base, base deeply cordate, with broad U-shaped sinus, usually wider than deep (base of blade hastate in young plants). Pseudanthial inflorescences with dimorphic involucral bracts, upper (distal) inconspicuous, green, and stipuliform, 2.5–5 × 1–2 mm, lower showy, whitish, 10–16 × 5–6 mm; staminate flowers usually 10; pistillate flowers 3. Staminate flowers with 10–11 stamens. Pistillate flowers with 6 unlobed sepals, sepals obovate-oblongate, 3–4 mm long; stylar column, clavate, straight, widest  $\sim 1/2$  to  $2/3$  of the way to the rounded tip, 4–9 mm long; stigma whitish, extending from tip to  $\sim 2/3$  length of stylar column. Seeds subspherical, 3.5–4.1 mm in diameter.

DISTRIBUTION.—Venezuela, Guyana, Surinam, French Guiana, and northern Brazil; 33 collections studied, 17 of which are from the Guianas (G:4, S:7, FG:6).

ECOLOGY.—In wet forest below 500 m. Found in forest margins and young secondary vegetation. Flowers and fruit collected year-round.

SELECTED SPECIMENS EXAMINED.—Guyana: Mazaruni Station, *FD 3923* (NY). Surinam: Marowijne, near Moengo, *Lindeman 6129* (K, NY, U); Oelemari River, 3°6'N, 54°33'W, *Wessels Boer 958* (U). French Guiana: Tampoc River, ~50 km SW of Saül, *Granville B.4846* (CAY, P, U, US); Village NaNouk, Litani and Maroni rivers, *Moretti 572* (CAY, U).

NOTES.—A member of sect. *Rhopalostylis*, this species lacks the prominent resiniferous inflorescence gland characteristic of the genus. Members of this common species previously have been assigned to *D. parvibracteata*, but they differ from the type of that species in having dimorphic involucral bracts and a whitish stigmatic surface that extends further down the style.

### 8. *Dalechampia magnoliifolia* Muell. Arg.

*Dalechampia magnoliifolia* Muell. Arg., Linnaea, 34:219, 1865. [Type: Brazil, Pará, *Martius* (holotype, B, destroyed; lectotype, M, designated by Webster & Armbruster, 1991).]

*Dalechampia roezliana* var. *amazonica* Ule, Verh. Bot. Vereins Prov. Brandenburg, 50:82, 1909.

*Dalechampia spathulata* var. *amazonica* (Ule) Pax & K. Hoffm., Pflanzennr., IV.147.XII, 68:11, 1919.

*Dalechampia amazonica* (Ule) Macbride, Candollea, 8:26, 1940. [Type: Brazil, Amazonas, Jurua Miry, *Ule 5865* (lectotype, G, designated by Webster & Armbruster, 1991).]

DESCRIPTION.—Monopodial subshrub 0.5–1.2 m tall. Leaves simple; stipules lance-ovate, 3–8 × 2–4 mm; petioles 0.2–1.0 cm long; blades chartaceous, narrowly oblong to oblanceolate, unlobed, 12–30 × 3.5–9.0 cm, base cordate. Pseudanthial inflorescence with showy pink involucral bracts, these ovate, 2.5–3.5 cm × 1.5–4.0 cm, with 3 major veins, base weakly clawed or truncate; usually 10 staminate flowers and 3 pistillate flowers; inflorescence gland bright yellow, dry, secreting spicy fragrance. Staminate flowers with 12–18 stamens. Pistillate flowers with columnar style, 4–8 mm long, tip very slightly dilated; stigmatic surface extending from the tip down most of the length of the stylar column. Seeds tuberculate, 6.5–7.0 mm long.

DISTRIBUTION.—In scattered sites in Amazonian Peru and Brazil, eastern Venezuela, and French Guiana; seven collections studied, three of which are from French Guiana.

ECOLOGY.—This diminutive subshrub occurs on floor of wet primary or secondary forest, below 250 m. The inflorescence gland secretes fragrance rather than resin. In Peru the flowers are pollinated by fragrance-collecting male euglossine bees (*Eulaema* and *Euglossa*; Armbruster et al., 1989). It probably flowers year-round.

SPECIMENS EXAMINED.—French Guiana: ~70 km SSW of Camopi, *Granville 317* (CAY); confluence of Litani and Marouini rivers, *Cremers 4998* (CAY, U); ~50 km W of Oiapoque, *Cremers 7075* (CAY).

### 9. *Dalechampia megacarpa* Armbruster

*Dalechampia megacarpa* Armbruster, Brittonia, 41:47, 1989. [Type: Venezuela, Bolívar, San Ignacio, *Armbruster et al. 85-115* (holotype, MO!; isotypes, ALA!, MY!, NY!, VEN!).]

DESCRIPTION.—Twining vine reaching canopy. Leaves simple; stipules lanceolate to ovate, 2.5–5 × 1.2–1.7 mm wide, commonly deciduous; petiole 3.5–10 cm long; blade chartaceous, ovate, unlobed, 7–27 × 3–20 cm, base truncate to deeply cordate. Pseudanthial inflorescences with moderately conspicuous green involucral bracts 10–15 × 4–6 mm; 7–10 staminate flowers and 3 pistillate flowers. Staminate flowers with 8–22 stamens. Pistillate flowers with 6 ovate unlobed sepals; stylar column cylindrical, straight, 4–6 mm long, apex not dilated, stigma extending nearly full length of stylar column. Capsules much larger than any other species, 35–40 mm in diameter.

DISTRIBUTION.—Collected only near San Ignacio, Edo. Bolívar, Venezuela, near San Carlos de Río Negro, Edo. Amazonas, Venezuela, and near Manaus, Brazil; five collections studied, from Venezuela and Brazil.

ECOLOGY.—Occurs in lowland wet forest below 500 m, at edge of forest or in forest canopy. The blue-green resin secreted by the inflorescence gland is collected by female *Euglossa* that

pollinate the flowers (Armbruster, 1988). Flowers and fruit present in December and January.

SELECTED SPECIMENS EXAMINED.—Venezuela: Amazonas, 15 km NE San Carlos de Rio Negro, *Liesner 7471* (VEN). Brazil: Amazonas, Manaus, km 8, BR17, *Rodrigues & Coelho 1801* (INPA).

NOTES.—This species has been found only in Guayanan and Amazonian Venezuela and Amazonian Brazil, but almost certainly occurs in Guyana.

### 10. *Dalechampia micrantha* Poepp.

*Dalechampia micrantha* Poepp., Nov. Gen. sp. pl., 3:19, 1841. [Type: Brazil, Amazonas, Ega (Tefé), *Poeppig 2807* (holotype, W; isotypes, K, P).]

*Megalostylis poeppigii* S. Moore, J. Bot., 54:208, 1916. [Type: Brazil, Amazonas, Ega (Tefé), *Poeppig* (BM).]

DESCRIPTION.—Twining vine reaching canopy. Leaves simple; stipules ovate, 2–3 × 1–2 mm, early deciduous prior to expansion of leaves; petioles 2–5 cm long; blades ovate, unlobed, 8–15 × 4–7 cm, base truncate, sometimes very shallowly cordate. Pseudanthial inflorescences with inconspicuous stipuliform involucre bracts 2–3 × 1.5–2 mm; usually 13 staminate flowers and 3 pistillate flowers. Staminate flowers with 4–9 stamens. Pistillate flowers with 5–6 unlobed sepals; stylar column clavate, slightly curved upwards, widest near blunt foveolate tip, stigma green, extending from tip to  $> 3/4$  length of stylar column. Fruit a capsule, sepals deciduous prior to fruit maturation.

DISTRIBUTION.—Venezuela (Bolívar), Surinam, Brazil (Amazonas), and Peru (Loreto); 20 collections studied, five are from Surinam.

ECOLOGY.—Occurs in moist to wet forests below 1000 m, forest edge or in secondary vegetation. Members of this species secrete a fragrance from the stigmatic surface of the pistillate flowers, attracting (in Venezuela) fragrance-collecting male *Euglossa* spp. (Hymenoptera: Apidae) that pollinate the flowers (Armbruster, unpublished observations). Flowers in late June (?), November through January, fruits present January to July.

SPECIMENS EXAMINED.—Surinam: SW of Lelydorp, *Lindeman et al. 214* (U); *Schomburgk 783* (P); *Schomburgk 784* (BM); *Schomburgk s.n.* (P); Jodensavanne-Mapane Creek, *Wessels Boer 454* (K, NY, U).

NOTES.—This species is a member of sect. *Rhopalostylis* and lacks the prominent resiniferous inflorescence gland characteristic of most of the genus.

### 11. *Dalechampia olympiana* Kuhlman & Rodrigues

*Dalechampia olympiana* Kuhlman and Rodrigues, Botanica, 5:1, 1954. [Type: Brazil, Amazonas, Manaus, *Rodrigues 225* (holotype, INPA).]

DESCRIPTION.—Twining vine, stems pilose-lanate with orange hairs. Leaves simple; stipules lanceolate, 6–10 mm long, ~2 mm wide; petioles 5–10 cm long; blades ovate, unlobed, 10–20 cm long, 6–13 cm wide, primary veins

orange-hirsute, base cordate, with narrow sinus. Pseudanthial inflorescences subsessile, with the two subequal, inconspicuous, green, stipuliform, hirsute, involucre bracts, ~12 staminate flowers, and 3 pistillate flowers. Staminate flowers with 9–14 stamens. Pistillate flowers with 4–6 sepals, these hirsute, unlobed, lance-linear, 3.0–4.0 mm long, 0.5–1.5 mm wide; stylar column weakly clavate, straight, 6–10 mm long, basal portions hirsute, stigmatic region covering  $1/2$ – $3/4$  of length. In fruit, pistillate pedicels 3–8 cm long, capsules hispid with yellow-brown hairs, ~18 mm in diameter; seeds fattened spheroidal, 5.0–5.5 mm long, 4.3–4.5 mm high, surface smooth, mottled brown and gray or black and gray.

DISTRIBUTION.—Apparently endemic to Amazonas and the Guianas; collected only in the Manaus region and recently in Guyana; five collections studied, of which one is from the Guianas (G:1).

ECOLOGY.—Pollination ecology is unknown. Flowers present in October; fruits present in May.

SPECIMENS EXAMINED.—Guyana: Maburo region, Pibiri compartment, plot 7, 05°1.95'N, 58°37.73'W, *Ek et al. 1187* (U).

NOTES.—An unusual member of section *Rhopalostylis* in having several, or more usually, numerous, subsessile pseudanthia in the axils of the leaves, and in having dense orange pubescence on the stems, petioles, and major leaf veins. Found in the Guianas in 1996; heretofore known only from the Manaus region of Amazonas, Brazil.

### 12. *Dalechampia papillistigma* Armbruster

*Dalechampia papillistigma* Armbruster, Brittonia, 41:49, 1989. [Type: Venezuela, Bolívar, Santa Elena de Uairen, 4°36'N, 61°15'W, *Armbruster et al. 87–155* (holotype, MO!; isotypes, ALA!, MY!, NY!, VEN!).]

DESCRIPTION.—Twining vine reaching lower canopy. Leaves palmately compound, 3–5 leaflets; stipules lanceolate 3–7 × 1–2 mm; petioles 2–10 cm long; blades chartaceous, that of center leaflet oblanceolate to obovate, 4–15 × 2–7 cm, base cuneate; blades of lateral leaflets similar but lanceolate to ovate with asymmetrical base. Pseudanthial inflorescences with moderately conspicuous, spatulate, green involucre bracts 5–8 × 3–4 mm; ~10 staminate flowers and 3 pistillate flowers. Staminate flowers usually with 70–80 stamens. Pistillate flowers with 6 sepals, each with 2–4 longitudinal lobes; stylar column cylindrical, straight, 2.7–3.3 mm long, with distinct capitate tip; stigmatic surface densely papillate, confined to the swollen tip of style.

DISTRIBUTION.—Known only from southeastern Edo. Bolívar, Venezuela, near Brazilian border; likely occurs in northern Brazil and southwestern Guyana. Endemic to region; two collections studied, both are from Venezuela.

ECOLOGY.—In moist forest 800–1000 m, at edge of riparian forest in savanna, reaching at least lower canopy. The inflorescence gland of this species secretes resin as a pollinator reward. Flowers and young fruit present in December.

SPECIMENS EXAMINED.—Venezuela: Santa Elena de Uairen, 4°37'N, 61°7'W, *Armbruster et al.* 87-154 (ALA).

NOTES.—Not closely related to any other species that we have examined.

### 13. *Dalechampia parvibracteata* Lanj.

FIGURE 7A,B

*Dalechampia parvibracteata* Lanj., *Recueil Trav. Bot. Néerl.*, 31:463, 1934. [Type: Guyana, Upper Demerara River, *Jenman 4088* (holotype, K; isotype, US!).]

DESCRIPTION.—Twining vine. Leaves simple, unlobed; stipules lanceolate, 3-7 × 1-2 mm; petioles 3-10 cm long; blades ovate, widest at about midpoint, 6-15 × 5-13 cm, base shallowly to deeply cordate, with U-shaped sinus, usually about as wide as deep. Pseudanthial inflorescences with inconspicuous, green, stipuliform, involucre bracts, 3-5 × 2-3 mm, and 3 pistillate flowers. Pistillate flowers with 6 unlobed sepals, these ovate-linear to obovate-linear, ~5 × 1-1.5 mm; stylar column clavate, straight, 5-9 mm long, with thin, elongated, pubescent stipe and expanded stigmatic region restricted to final 1/3 to 1/4 of length, tip rounded. Seeds 4.3-5.1 mm in diameter, flattened spheroidal.

DISTRIBUTION.—Known from Guyana, Venezuela (Bolívar), Brazil (Amazonas), and possibly Surinam; 16 collections studied, two are from Guyana.

ECOLOGY.—Flowers present November to June. Fruits present middle April to August (middle April in Guyana).

SPECIMENS EXAMINED.—Guyana: Berbice-Corentyne Region, Baba-Grant Sawmill, ~0.5 mi [0.8 km] above Cow Falls, *McDowell and Gopaul 2264* (ALA, US).

NOTES.—A member of sect. *Rhopalostylis*, this species appears to be most closely related to *D. heterobracteata*, from which it differs in having monomorphic involucre bracts and the stigma confined to the terminal 1/4 of the style. Nearly all specimens from the Guianas assigned to this species actually belong to *D. heterobracteata*.

### 14. *Dalechampia scandens* L.

*Dalechampia scandens* L., *Sp. pl.*, 1053, 1753. [Type: West Indies, illustrated by Plumier, *Plantarum Americanum, fasciculus 5*, pl. 101 (original plate at P).]

#### 14a. *Dalechampia scandens* var. *scandens*

FIGURE 8

*Dalechampia mollis* Vahl, *Eclog. amer.*, 3:44, 1807. [Type: Colombia, Santa Marta, *von Rohr* (C).]

*Dalechampia ruboides* Kunth in H.B.K., *Nov. gen. sp.*, 2:102, 1817. [Type: Venezuela, Angostura, *Humbolt & Bonpland* (P).]

*Dalechampia sidaefolia* Kunth in H.B.K., *Nov. gen. sp.*, 2:102, 1817. [Type: Venezuela, Pararuma Island and Angostura, *Humbolt & Bonpland* (P).]

*Dalechampia guianensis* Klotzsch, *London J. Bot.*, 2:43, 1843. [Type: British Guiana, *Schomburgk s.n.*]

*Dalechampia brevipes* Briq., *Annuaire Conserv. Jard. Bot. Genève*, 4:609, 1900. [Type: Colombia, Guanaguana, *Funk 64* (G).]

DESCRIPTION.—Twining or sprawling vine. Stems with sparse to dense, spreading, straw-colored to orangish pubescence. Leaves simple; stipules lanceolate to ovate, 3-8 × ~2 mm; petiole 2-8 cm long; blade chartaceous, ovate, usually 3-lobed, rarely unlobed, 3-10 × 3-13 cm, apex of each lobe acuminate, leaf base shallowly to deeply cordate, glabrescent above, sparsely to densely pubescent below. Inflorescence pseudanthial, on peduncle 2-6 cm long; the two bracts involucre, pale green to greenish white at anthesis, broadly ovate, 1.5-3.0 × 1.5-3.0 cm, with 5 major veins, apex divided into three lobes to ~1/2 length of bract; inflorescence contains 10 staminate flowers and 3 pistillate flowers; inflorescence gland secreting clear to whitish resin. Staminate flowers with 25-35 stamens. Pistillate flowers with calyx of 8-12 sepals, these pinnatifid; pistil with elongate stylar column, 4-8 mm long, tip only slightly and asymmetrically dilated, ~0.5 mm in diameter. Fruit a capsule; seeds spherical, mottled brown and gray, 3.5-4 mm in diameter, surface smooth.

DISTRIBUTION.—Widely distributed from Mexico to Argentina; widespread in the Guianas; 70 collections studied, 39 of which are from the Guianas (G:11, S:7, FG:21).

ECOLOGY.—Clambering vine of open areas, secondary scrub, and margins of dry to moist forest below 1000 m. This species is pollinated by resin-collecting female euglossine bees (*Euglossa*, *Eulaema*), megachilid bees (*Hypanthidium*), and stingless bees (*Trigona*) (*Armbruster*, 1985). Flowers year-round.

SELECTED SPECIMENS EXAMINED.—Guyana: Atkinson Field, Demerara, *Harrison 1769* (K, NY); road from Karanambo to Yupukari, 3°45'N, 59°20'W, *Maas et al.* 7222 (B, US). Surinam: Zuid River, 2 km above confluence with Lucie River, 3°20'N, 56°49'W-3°10'N, 56°29'W, *Irwin et al.* 55831 (NY, U, US); near Voltzberg, Saramacca, 4°41'N, 56°11'W, *Webster 24143* (NY, U). French Guiana: Camopi River, Belvedere Mt., *Granville 6940* (B, CAY, P); St. Laurent, Piste de Paul Isnard, *Skog & Feuillet 7427* (CAY, NY, P, U, US).

VERNACULAR NAMES.—Surinam: brongwirie (Surinamese), *Lanjouw & Lindeman 1114* (NY, U), from label; palaramau-loeloe (Carib), *Lanjouw & Lindeman 1807* (NY, U), from label.

NOTES.—This variety belongs to a highly variable species with numerous described infraspecific taxa and extensive ecotypic differentiation (*Pax and Hoffmann*, 1919b; *Armbruster*, 1985). The entire complex is in need of revisionary treatment.

#### 14b. *Dalechampia scandens* var. *fallax* Muell. Arg.

*Dalechampia scandens* var. *fallax* Muell. Arg. in *Martius, Fl. bras.*, 11(2):658, 1874b. [Type: Brazil, Pará, Santarem, *Spruce 199* (holotype, G).]

DESCRIPTION.—Twining or sprawling vine. Stems with dense, spreading, orange pubescence. Leaves simple; stipules lanceolate to ovate, 4-10 × 2-3 mm; petiole 3-10 cm long; blade chartaceous, ovate, usually 3-lobed, rarely unlobed, 6-15 × 6-20 cm, apex of each lobe acuminate, leaf base deeply

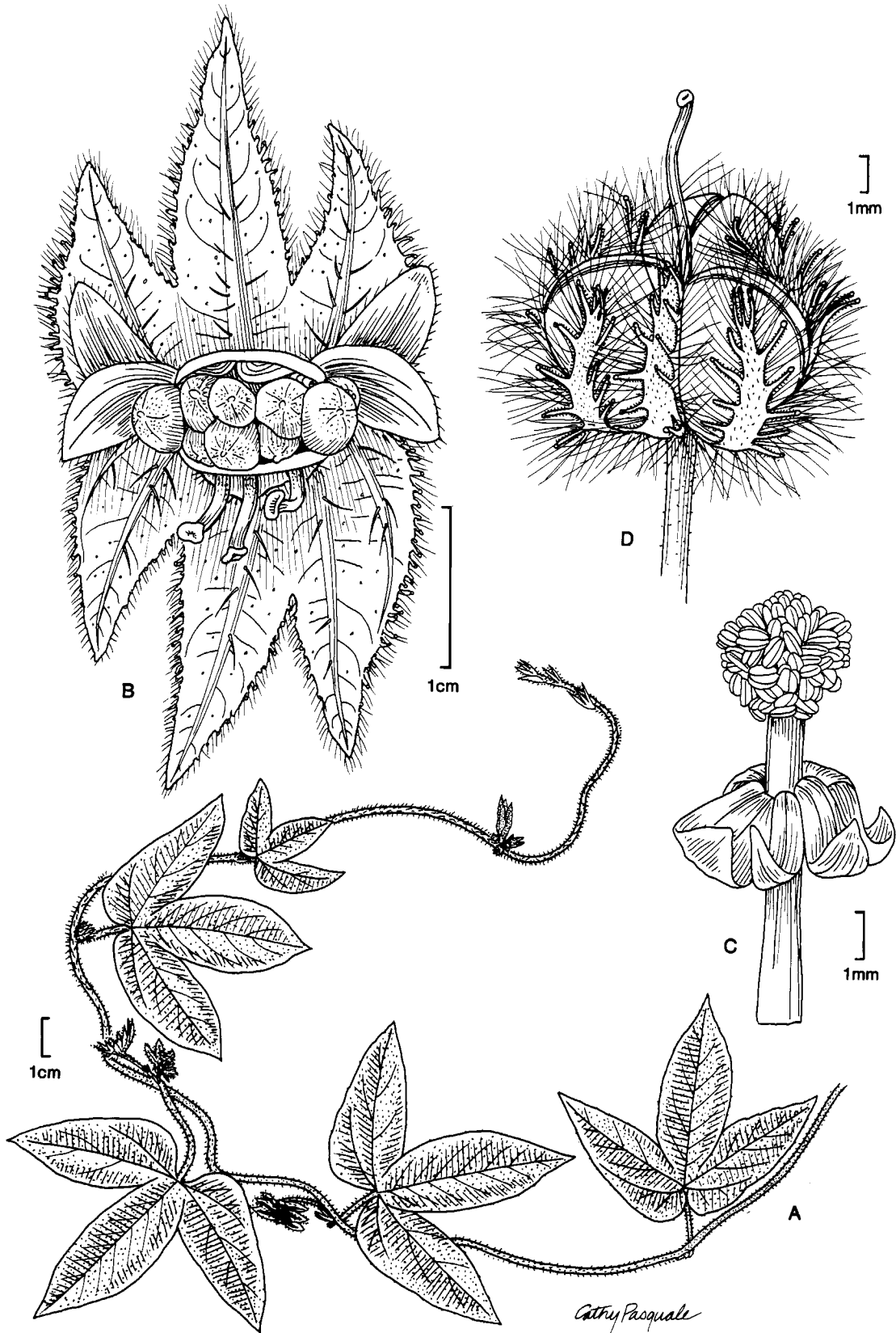


FIGURE 8.—*Dalechampia scandens* L. var. *scandens*: A, habit; B, inflorescence; C, staminate flower; D, capsule (based on Pittier 10351).

cordate, sparsely pubescent above, densely tomentose below. Inflorescence pseudanthial, on peduncle 8–12 cm long; the two bracts involucreal, white at anthesis, broadly ovate, 2.0–3.5 × 2.0–3.5 cm, with 5 major veins, apex divided into three lobes to near middle of bract; margins with glandular tentacular processes 1.0–1.5 mm long; inflorescence gland secreting clear to whitish resin. Staminate flowers with 25–35 stamens. Pistillate flowers with calyx of 8–12 sepals, these pinnatifid; pistil with elongate, umbraculiform styler column, 8–12 mm long, stigmatic surface confined to distal  $\frac{1}{3}$  of column; tip distinctly expanded, symmetrically peltate, ~2 mm in diameter.

DISTRIBUTION.—Occurs in southern Guyana and perhaps eastern Brazil (see “Notes” below); two collections studied, both are from Guyana.

SPECIMENS EXAMINED.—Guyana: Upper Takutu–Upper Essequibo Region, 5 km NNE of Dadanawa, *Gillespie 1955* (ALA); by Rupununi River, Turukwan, Rupununi, *Cook 44* (NY, U).

NOTES.—This taxon differs from *D. scandens* var. *scandens* in several characters, including the shape of the styler column, capitate tentacular processes on the bracts, and the capitate glandular margins of the pistillate involucellar bract. It is tentatively assigned to *D. scandens* var. *fallax*. However, this material differs from *D. scandens* var. *fallax* (as described by Mueller (1874b) and Pax and Hoffmann (1919b)) in having larger involucral bracts and pistillate involucellar bracts with capitate glandular margins. The taxon treated here should probably be recognized as a distinct species, although it may not be conspecific with the type material of *D. scandens* var. *fallax*. Formal recognition of this taxon must await a revisionary study of the *D. scandens* species complex.

### 15. *Dalechampia stipulacea* Muell. Arg.

*Dalechampia stipulacea* Muell. Arg., *Linnaea*, 34:221, 1865. [Type: Peru, *Pavon* (holotype, G).]

DESCRIPTION.—Twining vine sometimes reaching lower canopy. Leaves simple; petiole 2–6 cm long; blade chartaceous, usually ovate, rarely lanceolate, usually 3-lobed, 5–12 × 6–14 cm, apex of each lobe narrowly acuminate, leaf base deeply cordate, sparsely pubescent above and below, margins usually capitate glandular; stipules lanceolate-ovate, 10–20 × 3–5 mm, margins capitate glandular. Inflorescence pseudanthial; the two bracts involucreal, pale green at anthesis, broadly ovate, tip deeply 3-lobed, 4–6 × 2–4 cm, sparsely pubescent, margins usually capitate glandular; resiniferous gland secreting yellow resin. Staminate flowers with 30–~50 stamens. Pistillate flowers with calyx of 10–12 sepals, these pinnatifid, capitate glandular, hispid; pistil with elongate styler column, 10–15 mm long, tip moderately dilated. Fruit a capsule, surface glabrescent; seeds spherical, mottled brown and gray, ~4 mm in diameter, surface smooth.

DISTRIBUTION.—Widespread from western Venezuela, Colombia, and Peru, south to southern Brazil, Argentina, and

Paraguay. Absent or rare in most of Amazonia and the Guianas. Locally distributed in French Guiana, thus far known only from Saül area; 15 collections studied, of which two are from French Guiana.

ECOLOGY.—In open areas, including secondary vegetation and edges of moist to wet forest, below 1000 m elevation. The species is distinctive in secreting resin from vegetative parts; this resin inhibits feeding by both generalist and specialist insect herbivores and presumably plays a role in defense (Armbruster, unpublished observations). The inflorescence gland secretes copious yellow resin that is collected by pollinating female euglossine bees (*Eulaema*) in Venezuela. In French Guiana we saw only visitation by *Hypanthidium* sp. (Megachilidae), which are too small to be efficient pollinators. Flowers have been collected in August and June in French Guiana; it appears to flower year-round in Venezuela.

SPECIMENS EXAMINED.—French Guiana: Route de Belizon between Eaux Claires and entrance to Boeuf-Mort trail, *Mori et al. 23721* (CAY); ~4 km north of Saül, Route de Belizon at junction with Boeuf Mort trail, *Armbruster & Edwards 95-03* (CAY, ALA).

NOTES.—This species is distinctive in the Guianan region in having stipules, involucreal bracts, and leaves with strongly capitate glandular margins. In some plants the leaf margins are eglandular, but even in these plants the stipules have glandular appendages.

*Dalechampia stipulacea* has been only recently collected from the Guianas, from just one small area near Saül, French Guiana. Judging from collections, the species is generally absent from the Guianas and Amazonia. The nearest populations we are aware of are ~1500 km away in Brazil and ~1800 km away in western Venezuela. Surprisingly, the Guianan material closely resembles the Venezuelan material. It is not known whether this apparent tremendous disjunction represents incomplete collecting in intervening regions, strange biogeographic history, or recent introduction (by miners?) in the Saül area.

### 16. *Dalechampia tiliifolia* Lam.

*Dalechampia tiliifolia* Lam., *Encycl.*, 2:257, 1786. [Type: possibly Peru, *Herb. Jussieu* (holotype, P).]

*Dalechampia peruviana* Lam., *Encycl.*, 2:257, 1786. [Type: Peru, *Herb. Jussieu* (P).]

*Dalechampia heterophylla* Vahl, *Ecl. amer.*, 3:44, 1807. [Type: Cayenne, *Von Rohr* (C).]

*Dalechampia pruriens* Griseb., *Fl. Brit. W. I.*, 51, 1859. [Type: Trinidad, *Crueger* (GOET).]

DESCRIPTION.—Twining vine sometimes reaching lower canopy. Leaves simple; stipules lance-linear, 3–7 × ~1 mm; petiole 2–8 cm long; blade chartaceous, usually ovate, rarely lanceolate, usually 3-lobed mixed with unlobed when in bloom, 6–15 × 4–13 cm, apex of each lobe acuminate, leaf base shallowly to deeply cordate, sparsely pubescent above, velutinous below. Inflorescence pseudanthial; the two bracts involu-



cral, cream-white at anthesis, broadly ovate, tip shallowly 3-lobed, 3–6.5 × 3–6 cm, velutinous, with 7–9 major veins; resiniferous gland secreting yellow resin. Staminate flowers with ~40 stamens. Pistillate flowers with calyx of 10–13 sepals, these pinnatifid, densely hispid; pistil with elongate stylar column, 6–12 mm long, tip asymmetrically dilated to umbraculiform. Fruit a capsule, surface sparsely to densely hispid; seeds spherical, mottled brown and gray, ~5 mm in diameter, surface smooth.

**DISTRIBUTION.**—Widespread from Mexico to southern Brazil. Widespread in unforested parts of the Guianas; 50 collections studied, of which 33 are from the Guianas (G:1, FG:32).

**ECOLOGY.**—In open areas, secondary scrub, and edge of dry to moist forest below 1800 m. The inflorescence glands secrete yellow resin that is collected by pollinating female euglossine bees (*Eulaema*, *Euglossa*) (Armbruster and Herzig, 1984). Flowers in the dry season in Mesoamerica; flowers collected in the Guianas throughout the year; fruits mostly March to June.

**SELECTED SPECIMENS EXAMINED.**—Guyana: Iramaipang, Kanuku Mts., *FD 5978* (K, NY). French Guiana: near Cayenne, *Cremers 9429* (B, CAY, MO, NY, P, US); route to Stoupan, Ile de Cayenne, *Feuillet 1754* (CAY, P); Mahury Mt., Rorota, *Granville 260* (CAY, P, U); Mt. St. Martin, Cayenne Island, 4°56'N, 52°17'W, *Hoff 5357* (B, CAY, NY, P, US); route to Stoupan, Ile de Cayenne, *Oldeman B-802* (CAY, U); north of Saül, *Prevost 1808* (CAY, U, US).

**NOTES.**—Very closely related to *D. affinis*, from which it differs by having at least some 3-lobed leaves when in bloom, involucre bracts that are always shallowly 3-lobed and often nearly as wide as long, and style tips asymmetrically dilated rather than umbraculiform.

#### 17. *Dalechampia* aff. *cissifolia* Poepp.

*Dalechampia* aff. *cissifolia* Poepp., Nov. gen. sp. pl., 3:20, 1841. [Type: Peru, Maynas, Yurimaguas, *Poeppig 2085* (holotype, W; isotype, G).]

**DESCRIPTION.**—Twining or sprawling vine. Leaves usually compound, rarely simple; stipules lanceolate, 3–5 × 0.5–1.0 mm; petiole 0.5–2.0(4.5) cm long; blade chartaceous, leaflets lanceolate, 2.5–6.5(8) × 0.5–2 cm, apex of each leaflet acute, central base cuneate, laterals oblique, glabrescent to sparsely pubescent above and below. Inflorescence pseudanthial, on peduncle 0.5–2.0 cm long; the two bracts involucre, leaf-green at anthesis, broadly ovate, 1.0–1.5 × 0.8–1.5 cm, with 5 major veins, apex entire or divided into three lobes to ~1/4 to 1/2 length of bract; inflorescence contains ~10 staminate flowers and 3 pistillate flowers; inflorescence gland secreting resin. Pistillate flowers with calyx of 8–12 sepals, these pinnatifid; pistil with elongate stylar column, 1.5–3 mm long, tip only slightly and asymmetrically dilated. Fruit a capsule; seeds spherical, mottled brown and gray, ~4 mm in diameter, surface smooth.

**DISTRIBUTION.**—Material referable to this taxon has been collected only in Guyana; two collections studied, both are from Guyana.

**SPECIMENS EXAMINED.**—Guyana: Upper Takutu, Upper Essequibo Region, SE Kanuku Mts., *Gillespie 1832*; Upper Takutu, Upper Essequibo Region, near Surama village, *McDowell 2037*.

**NOTES.**—The *Dalechampia cissifolia/triphylla* complex is badly in need of revision. Until such a revision is completed it is difficult to determine the taxonomic status of this taxon. It is almost certainly distinct at the species level from *D. cissifolia*.

#### 18. *Dalechampia* aff. *triphylla* Lam.

*Dalechampia* aff. *triphylla* Lam., Encyl., 2:258, 1786. [Type: Brazil, *Dombey* (holotype, P [Herb. Jussieu 16292]; isotype, NY).]

**DESCRIPTION.**—Twining or sprawling vine. Leaves usually compound, rarely simple; stipules lanceolate, 4–7 × 1.0–1.5 mm; petiole 4–10 cm long; blade membranous to chartaceous, leaflets lanceolate, 4–10 × 1.5–3 cm, apex of each leaflet acute, central base cuneate, laterals oblique, glabrescent to sparsely pubescent above and below. Inflorescence pseudanthial, on peduncle 1–2 cm long; the two bracts involucre, leaf-green at anthesis, broadly ovate, 1.2–1.5 × 1.5–2.0 cm, with 5 major veins, apex divided into three lobes to ~1/3 to 1/2 length of bract; inflorescence contains ~10 staminate flowers and 3 pistillate flowers; inflorescence gland secreting clear resin. Pistillate flowers with calyx of usually 6 sepals, these with broad rachis, width > 1/4 length, and shallowly to deeply lobed, densely ciliated margins; pistil with elongate stylar column, 4–5 mm long, tip only slightly and asymmetrically dilated. Fruit a capsule; seeds spherical, mottled brown and gray, ~3 mm in diameter, surface smooth.

**DISTRIBUTION.**—Occurs in Surinam and French Guiana; four collections examined, all are from the Guianas (S:3, FG:1).

**ECOLOGY.**—Occurs in disturbed sites in lowland forests. Floral resin is collected in Surinam by female *Hypanthidium* cf. *panamense* (Megachilidae), which pollinate the flowers (Armbruster and Herzig, unpublished observations). Apparently flowers year-round.

**SPECIMENS EXAMINED.**—French Guiana: St. Laurent, piste de Paul Isnard, *Billiet & Jadin 1613* (CAY). Surinam: *Lindeman et al. 655* (U); Brownsberg Nature Park, *Webster & Mohr 24122* (U); Brownsberg Nature Park, *Armbruster & Herzig 85–103* (ALA).

**NOTES.**—The *Dalechampia cissifolia/triphylla* complex is badly in need of revision. Until such a revision is completed it is difficult to determine the status of this taxon, except that it is definitely not conspecific with *D. triphylla*. In many respects this taxon is intermediate between *D. triphylla* and *D. cissifolia*, but the nature of the pistillate sepals indicates closer affinity to *D. triphylla*.

#### 4. Genus *Haematostemon* (Muell. Arg.) Pax & K. Hoffm.

*Haematostemon* (Muell. Arg.) Pax & K. Hoffm., Pflanzenr., IV.147.IX, 68:31, 1919a.

*Astrocooccus* sect. *Haematostemon* Muell. Arg., Linnaea, 34:158, 1865. [Type: *Haematostemon coriaceus* (Baill.) Pax & K. Hoffm.]



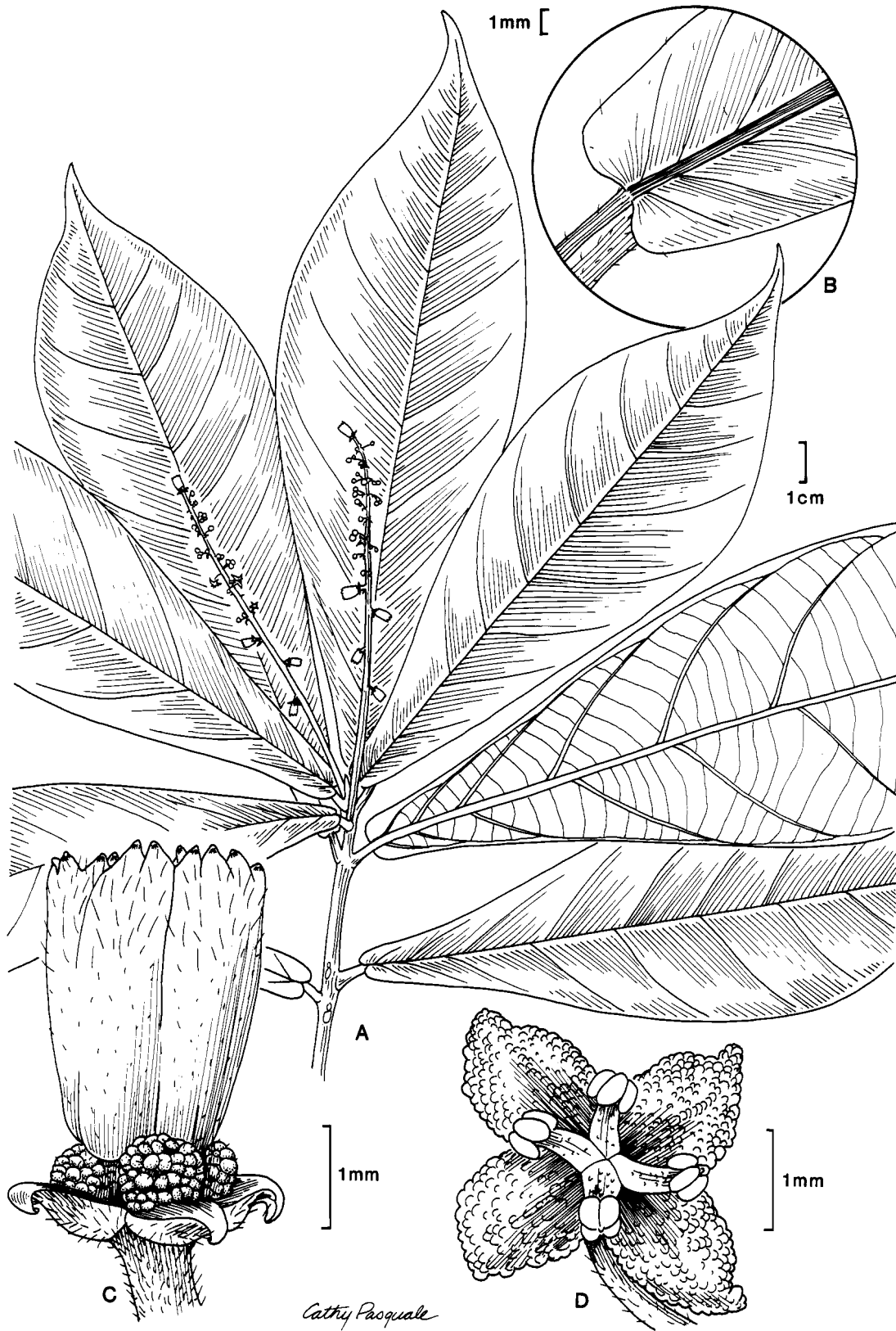


FIGURE 9.—*Haematostemon guianensis* Sandwith: A, habit; B, leaf blade base, adaxial surface; C, pistillate flower (note verrucate ovary lobes and massive truncate style); D, staminate flower (note verrucate-papillate inner surface of sepals) (based on *Fanshawe 2869 = FD 6016*).

DESCRIPTION.—Shrubs or small trees, monoecious, latex absent. Leaves simple, alternate, petiolate; stipules small, deciduous; blade pinnately veined, margin entire to serrate; glands absent. Inflorescence a racemose thyrse, axillary, bisexual; lower nodes with solitary pistillate flowers or bisexual cymes with central pistillate flower, upper nodes with unisexual cymes of staminate flowers, axis terminating in a single pistillate flower; bracts narrowly triangular, small, eglandular. Staminate flowers pedicellate; sepals 4, valvate; corolla and disc absent; stamens 4; filaments conical, dilated and connate at base, with dilated bases sometimes resembling an intrastaminal pseudodisc (e.g., *H. coriaceus*); pistillode absent. Pistillate flowers pedicellate; sepals 4 (or more on terminal flower); corolla and disc absent; ovary 3-locular, distinctly 3-lobed with carpels globose, verrucate; styles completely connate into massive, elongate cup-shaped structure with a narrow hollow center, apex truncate and very shortly 3-lobed, with lobes notched and papillose. Fruit (known only in *H. coriaceus*) capsular?, distinctly 3-lobed, 3-carpellate. Seeds unknown.

DISTRIBUTION.—Two species, one in Guyana, one in Venezuelan Guayana.

LITERATURE.—Pax and Hoffmann (1919a:31–32).

### 1. *Haematostemon guianensis* Sandwith

FIGURE 9

*Haematostemon guianensis* Sandwith, Kew Bull., 1950:133, 1951. [Type: Guyana, Eagle Mountain, Fanshawe 1123 = FD 3859 (holotype, K!; isotypes, FDG!, K!, NY!, U!).]

DESCRIPTION.—Tree to 6 m tall. Branchlets sparsely pubescent to glabrate, pubescent at tip. Petiole 3–7 mm long, pubescent; blade thinly subcoriaceous, oblanceolate, 11–26 × 4–7.5 cm long, apex acuminate, base cuneate and very narrowly auriculate, glabrescent. Inflorescence 5–15 cm long, slender, axes pubescent; pistillate flowers 2–5, solitary at basal nodes, staminate flowers numerous in condensed cymes above, single pistillate flower at apex of inflorescence axis; bracts 1–1.5 mm long. Flowers pink-brown. Staminate pedicel 2–2.5 mm long, sparsely pubescent; bud subglobose, 1–1.5 mm long; sepals ovate, 1.2–1.5 × ~1 mm, apex acute, glabrate, inner surface verrucate-papillate; filaments 0.5–0.7 mm long, dilated to 0.2–0.3 mm wide at base, pointed at apex. Pistillate pedicel 1–2.5 mm long, densely pubescent; sepals oblong-lanceolate, ~1.5 mm long, outer surface sparsely pubescent; ovary distinctly 3-lobed, ~0.8 × 1.5–2 mm, densely verrucate, glabrous; stylar column oblong-obovoid, 2.5–3.5 × ~2 mm, truncate at apex with broad lobes bearing horn-like papillae at corners. Fruit unknown.

DISTRIBUTION.—Endemic to Guyana, where it is known only from near Mahdia in central Guyana; three collections studied.

ECOLOGY.—Forest understory tree collected in kakaralli

(*Eschweilera* spp.)-clump wallaba (*Dicymbe* spp.) forest on escarpment slope on red lateritic soil. Flowers and young fruits reported in January and March.

SPECIMENS EXAMINED.—Guyana: Mahdiana Mt., Potaro, Atkinson 114 (BM); Mahdiana Mt., Potaro, Fanshawe 2869 = FD 6016 (FDG, K, NY, U, US).

NOTES.—*Haematostemon* may be distinguished by its small tree or shrub habit, staminate flowers with four sepals and four stamens, and styles that are connate into a massive narrowly cup-shaped stylar column. *Haematostemon coriaceus* (Baill.) Pax & K. Hoffm., the only other member of the genus, is endemic to the Río Guainia area of Amazonas state, Venezuela. This species may be distinguished from *H. guianensis* by its smaller, narrowly ovate leaf blades and shorter inflorescences. The related monotypic genus *Astrocooccus*, endemic to the upper Río Negro region of Venezuela and Brazil, may be distinguished by its 4-segmented extrastaminal disc, ovoid-urceolate stylar column, and conspicuously horned carpels.

### 5. Genus *Plukenetia* L.

*Plukenetia* L., Sp. pl., 1192, 1753. [Type: *Plukenetia volubilis* L.]

*Apodandra* Pax & K. Hoffm., Pflanzenz., IV.147.IX, 68:20, 1919a. [Lectotype: *Apodandra lorentensis* (Ule) Pax & K. Hoffm.]

*Elaeophora* Ducke, Arch. Jard. Bot. Rio de Janeiro, 4:112, 1925. [Type: *Elaeophora abutifolia* Ducke.]

DESCRIPTION.—Lianas or twining vines, monoecious or rarely dioecious; latex absent. Leaves simple, alternate, petiolate; stipules small, deciduous; blade pinnately or palmately veined, margin subentire to serrulate; 1 to several pairs of flat laminar glands present near base on adaxial blade surface; scattered laminar glands often present on abaxial blade surface, rarely present on adaxial surface (only in *P. supraglandulosa*). Inflorescence a racemose thyrse, axillary or terminal on short shoot, bisexual with pistillate flower(s) at base and staminate flowers above in condensed cymes or less often unisexual; bracts triangular, small, eglandular. Staminate flower pedicellate; sepals 4–5, valvate; corolla absent; disc interstaminal, segmented or annular, or often absent; stamens 15–40, free; filaments short to elongate or anthers sessile; pistillode absent. Pistillate flower pedicellate; sepals 4; corolla absent; disc absent; ovary 4-locular, 4-angled to deeply 4-lobed, carpel lobes carinate or with tubercle or horn; styles partly to completely connate, stylar column cylindrical to globose or obovoid. Fruit a 4-seeded capsule or berry, subglobose to deeply 4-lobed; carpels carinate or with central tubercle or horn. Seeds subglobose, ovoid, or lenticular and often laterally compressed, ecarunculate, surface smooth or roughened.

DISTRIBUTION.—Seventeen species, 12 in the Neotropics, four in Africa and Madagascar, one in Asia; five species in the Guianas.

LITERATURE.—Pax and Hoffmann (1919a:11–24); Gillespie (1993b).

**Key to the Species of *Plukenetia***

1. Leaf blades pinnately veined, elliptic in shape, acute, obtuse, or rounded at base; scattered laminar glands present on lower surface of blade . . . . . 2  
 Leaf blades palmately veined or 3-veined at base, ovate or cordiform in shape, cordate, truncate, or rounded at base; laminar glands absent on lower surface of blade (or very small and marginal in *P. verrucosa*) . . . . . 3
2. Stylar column slender-cylindrical, 2–4 mm long; ovary and capsule with pointed horn on each carpel; androecium consisting of 15–25 anthers sessile on globose receptacle; scattered laminar glands absent on upper surface of leaf blade . . . . . 1. *P. lorentensis*  
 Stylar column stout-cylindrical, ~1.6 mm long; ovary and capsule with rounded tubercle on each carpel; androecium consisting of outer whorl of 4 stamens with filaments, and inner cluster of 6–9 anthers sessile on globose receptacle; numerous scattered laminar glands present on upper surface of leaf blade . . . . . 3. *P. supraglandulosa*
3. Styles completely connate into subglobose or obovoid column; stamens in outer whorl with filaments, inner anthers sessile; fruit 4-lobed, less than 1.5 cm in diameter, dehiscent . . . . . 4. *P. verrucosa*  
 Styles connate into cylindrical column, free at apex; all stamens with filaments; fruit greater than 2.5 cm in diameter . . . . . 4
4. Stylar column 15–30 mm long, arms ~1 mm long; fruit 4-lobed, 2.5–4(–6) cm in diameter, dehiscent; staminate bud subglobose; filaments conical, ~0.5 mm long; leaf base cordate or truncate . . . . . 5. *P. volubilis*  
 Stylar column 3–7 mm long, arms 1.5–2.5 mm long; fruit subglobose, squarish in cross-section, 6–11 cm in diameter, indehiscent; staminate bud narrowly oblong-ellipsoid; filaments slender, 2–3 mm long; leaf base rounded or obtuse . . . . . 2. *P. polyadenia*

**1. *Plukenetia lorentensis* Ule**

*Plukenetia lorentensis* Ule, Verh. Bot. Vereins Prov. Brandenburg, 81, 1908. [Type: Peru. Loreto. Iquitos, *Ule 6837* (isotype, G!).]  
*Apodandra lorentensis* (Ule) Pax & K. Hoffm., Pflanzenr., IV.147.IX, 68:21, 1919a.

DESCRIPTION.—Vine or liana, monoecious. Young stems tomentose, becoming sparsely pubescent, often twining. Petiole 0.5–2 cm long, tomentose; blade chartaceous, elliptic, 6–12(–16) × 3–7(–9) cm, apex acuminate, base acute to obtuse and shortly decurrent, margin serrulate, glabrescent to sparsely pubescent on major veins above and below, pinnately veined; basilar glands 2–4 pairs, circular, ~1 mm in diameter, or sometimes confluent into a single elongate pair, ~3 mm long, on decurrent leaf base; scattered laminar glands circular, ~0.5 mm wide, near margin. Inflorescences axillary, racemose, 1–6 cm long, axes sparsely to densely tomentose; pistillate flower single at base, staminate flowers in condensed cymes above; bracts ovate-triangular, ~1 mm long, sparsely pubescent. Staminate pedicel 4–8 mm long, tomentose; bud subglobose, ~1.5 mm long, apex obtuse; sepals 4, ovate-elliptic, 2–2.5 mm long, sparsely pubescent; anthers 15–25, sessile on globose receptacle. Pistillate pedicel 2–3 mm long, tomentose; sepals triangular, ~0.7 mm long, sparsely pubes-

cent, appressed to ovary; ovary 4-horned, 1–1.5 × 2–3 mm, densely tomentose except for horns; style cylindrical, 2–4 × ~0.5 mm, sparsely tomentose; stigma 4-lobed, ~1 mm wide. Capsule 4-lobed, 0.5–0.7 × 1–1.2 cm, puberulent, dehiscent, each carpel lobe with pointed horn, 3–6 mm long. Seeds subglobose to broadly lenticular, 5–6 × 3.5–5 × 4.5–5.5 mm, mottled pale and dark brown with coarse dark brown raised reticulations.

DISTRIBUTION.—Colombia (Amazonas), Venezuela (Amazonas, Bolívar), Guyana, Peru (Loreto, San Martín), Bolivia (Beni), and Brazil (Amazonas, Mato Grosso, Rondônia); in Guyana known only from the New River area; 53 collections studied, of which one is from Guyana.

ECOLOGY.—Occurs in moist to wet lowland forest, below 700 m. The single flowering and fruiting collection known from Guyana was made in September.

SPECIMENS EXAMINED.—Guyana: Kanasenay, *Guppy 203* = *FD 7179* (NY-3 sheets).

VERNACULAR NAME.—Guyana: Chichinat (*FD 7179*).

**2. *Plukenetia polyadenia* Muell. Arg.**

FIGURE 10A-D

*Plukenetia polyadenia* Muell. Arg. in Mart., Fl. bras., 11(2):334, 1874a. [Type:



FIGURE 10.—*Plukenetia polyadenia* Muell. Arg. and *P. volubilis* L. A-D, *P. polyadenia*: A, habit, showing axillary staminate inflorescences; B, pistillate inflorescences in leaf axils; C, staminate flower (A,C based on *Fanshawe 3383 = FD 6947*, NY; B,D based on *Black 52-14173*, P); E, *P. volubilis*: E, pistillate flower (based on *Zarucchi 2378*, US).

Brazil, Prov. Maynas, *Poeppig 2385* (holotype, W, photo F32544!, fragment at FI; isotype, G!).]

*Elaeophora polyadenia* (Muell. Arg.) Ducke, Arch. Jard. Bot. Rio de Janeiro, 5:146, 1930.

*Elaeophora abutifolia* Ducke, Arch. Bot. Rio de Janeiro, 4:112, 1925. [Syntypes: Brazil, near Belém, *Ducke HJBR 17892* (not seen); Tajapurú R., *Ducke HJBR 17893* (isosyntype, P!); Xingu R., *Kuhlmann HJBR 17895* (isosyntype, U!).]

*Plukenetia abutifolia* (Ducke) Pax & K. Hoffm., Pflanzenfam., ed. 2, 19c:141, 1931.

**DESCRIPTION.**—Liana climbing to canopy, dioecious or sometimes monoecious. Branchlets glabrous to sparsely puberulous, often twining. Petiole 1.5–5 cm long, glabrous; blade chartaceous to subcoriaceous, elliptic to ovate-elliptic, 7–11 (–14) × 4–7 (–10) cm, apex obtuse-acuminate with acumen slender 0.6–1.5 cm long, base rounded to obtuse, glabrous, 3-veined at base; basilaminar glands 1 pair (rarely 2 pairs), transversely elliptic, ~1.5–2 mm wide, with small knob between; scattered laminar glands absent. Inflorescences axillary, racemose or sometimes paniculate, usually unisexual, axes puberulous; staminate inflorescence 5–25 (rarely to 35) cm long, flowers numerous on scorpioid or dichasial-scorpioid cymose lateral branches 0.2–2 cm long, pistillate flowers occasionally present at basal-most 1–2 nodes on an otherwise staminate inflorescence; pistillate inflorescence 1.5–3 (rarely to 7) cm long, flowers 3–4 (–10), 1 or rarely 2 per lateral cyme branch, these 1–3 mm long; bracts triangular, ~1 mm long, apex acuminate. Staminate pedicel 2–4 mm long; bud narrowly oblong-ellipsoid or oblong-ellipsoid, ~3 mm long, apex acute; sepals 4, narrowly oblong, 3–4 mm long, apex acute, glabrous, reflexed at anthesis; stamens 20–25 on convex scaly receptacle; filaments 2–3 mm long, slender, attenuate at apex. Pistillate pedicel 0.5–1 mm long, glabrous to sparsely puberulent; sepals 4, triangular, 0.5–1 mm long, glabrous, appressed to ovary; ovary 4-angled, ~1.5 × 2 mm, not distinctly winged or lobed, glabrous; styles connate into a narrow-conical column, 3–7 mm long, free at apex, arms 1.5–2.5 mm long, divergent. Infructescence up to 8 cm long; berry subglobose, quadrangular in cross section, each angle distinctly keeled, 6–10 cm long × 6–11 cm in diameter, glabrous, fleshy, indehiscent, with broad conical apical protuberance ~0.5 cm long. Seeds ovoid, 4.9–5.6 × 3.3–3.7 × 3.0–3.5 cm, apex narrowed, base rounded, dull brown, surface rough.

**DISTRIBUTION.**—Widespread in the Guianas, eastern Venezuela, and the Amazon basin in Ecuador, Peru, Bolivia, and Brazil; 46 collections studied, of which 15 are from the Guianas (G:6, S:3, FG:6).

**ECOLOGY.**—Canopy liana in moist to wet lowland or lower montane forest, sea level to ~1000 m. Flowers reported between February and August in the Guianas, fruits in August and October. Seed germination is epigeal and cryptocotylar, i.e., the cotyledons of seedlings are above ground but remain hidden within the seed coat (Gillespie, unpublished observations).

**SPECIMENS EXAMINED.**—Guyana: Demerara, introduced from Fort Island, *Beckett & Kortright 8640* (BRG, K, U); Camaria Falls, Cuyuni R., *Fanshawe 3383 = FD 6947* (FDG,

K, NY); Mt. Ayanganna, *Tillet et al. 44950* (MO, NY, US); Mt. Ayanganna, *Tillet et al. 44954* (NY); Kamarang R., *Tillet & Tillet 45834* (NY, US); Oko Creek, Cuyuni R., *Tutin 359* (K, U, US). Surinam: Emmaketen, *Daniels & Jonker 1109* (US); along road near Moengo tapoe, *Lindeman 6134* (AAU, DAV, F, K, U); Jodensavanne-Mapane Kreek area, *Schulz 7284* (MO, U, US). French Guiana: vieille route de St. Laurent-Saut Sabbut, 10 Apr 1971, *Fouqué s.n.* (CAY); Saül, *Granville B.4413* (CAY); Saül, *Grenand 647* (CAY); Saül, *Moretti 461* (CAY); Saül, *Mori 15673* (NY, fruit only); Saül, *Mori & Gracie 18668* (CAY, K, US).

**USES.**—According to Ducke (1925) seeds are sold for their oil in local markets in the Brazilian state of Pará.

**NOTES.**—Ducke (1925, 1930) considered the species to be dioecious with dimorphic unisexual inflorescences in contrast to the bisexual inflorescences of all other species in the genus. The majority of collections examined are either staminate or in fruit. Two collections have pistillate flowers only, whereas three collections have bisexual inflorescences (e.g., *Schulz 7284*) (Gillespie, 1993b). Therefore, the species appears to be at least sometimes monoecious. The above description of pistillate inflorescences was taken from two Brazilian collections (*Black 52-14137*; *Ducke 17893*).

### 3. *Plukenetia supraglandulosa* L.J. Gillespie

FIGURE 11

*Plukenetia supraglandulosa* L.J. Gillespie, Syst. Bot., 18:589, figs. 2, 7, 8, 10, 1993. [Type: French Guiana, Sommet Tabulaire, zone centrale, versant occidental, about 40 km SE de Saül, *Granville 3626* (holotype, US!; isotypes, CAY!, U!).]

**DESCRIPTION.**—Liana, monoecious. Branches slender, branchlets puberulous. Petiole 0.5–2.0 cm long, puberulous; blade chartaceous, elliptic or ovate-elliptic, 7–13 × 3–8 cm, margin serrulate, apex slender-acuminate with acumen 0.5–1 cm long, base acute, glabrescent except lower midrib puberulous, major veins and midrib sometimes sparsely puberulous below, pinnately veined, secondary veins distinctly looped; basilaminar glands in 1–3 pairs, circular or elliptic; laminar glands circular, on both surfaces, 10–20 near margin on abaxial surface, 8–18 scattered between midrib and margin on adaxial surface. Inflorescences axillary, racemose, 2–8 cm long, axes puberulous, green; pistillate flower single at base, staminate flowers numerous in very condensed cymes above; bracts triangular, ~1 mm long. Staminate pedicel 3.5–4.5 cm long, densely puberulous; bud subglobose, ~1 mm long or less, apex rounded or broadly obtuse; sepals 4, elliptic, 1–1.3 mm long, apex acute and thickened, reflexed; disc 4-lobed, located between outer stamen whorl and inner stamen cluster; androecium of 4 outer stamens with filaments 0.3–0.4 mm long and 6–9 sessile anthers on globose receptacle. Pistillate pedicel 6–12 mm long, puberulous; sepals 4, triangular, ~1 mm long; ovary 4-winged, ~1 × 2 mm, densely puberulous, wings rounded; style stout-cylindrical, ~1.6 × 0.6 mm, sparsely puberulous. Capsule 4-lobed, ~7 × 15 mm, sparsely puberulous, dehiscent, pendant, each carpel lobe with single blunt

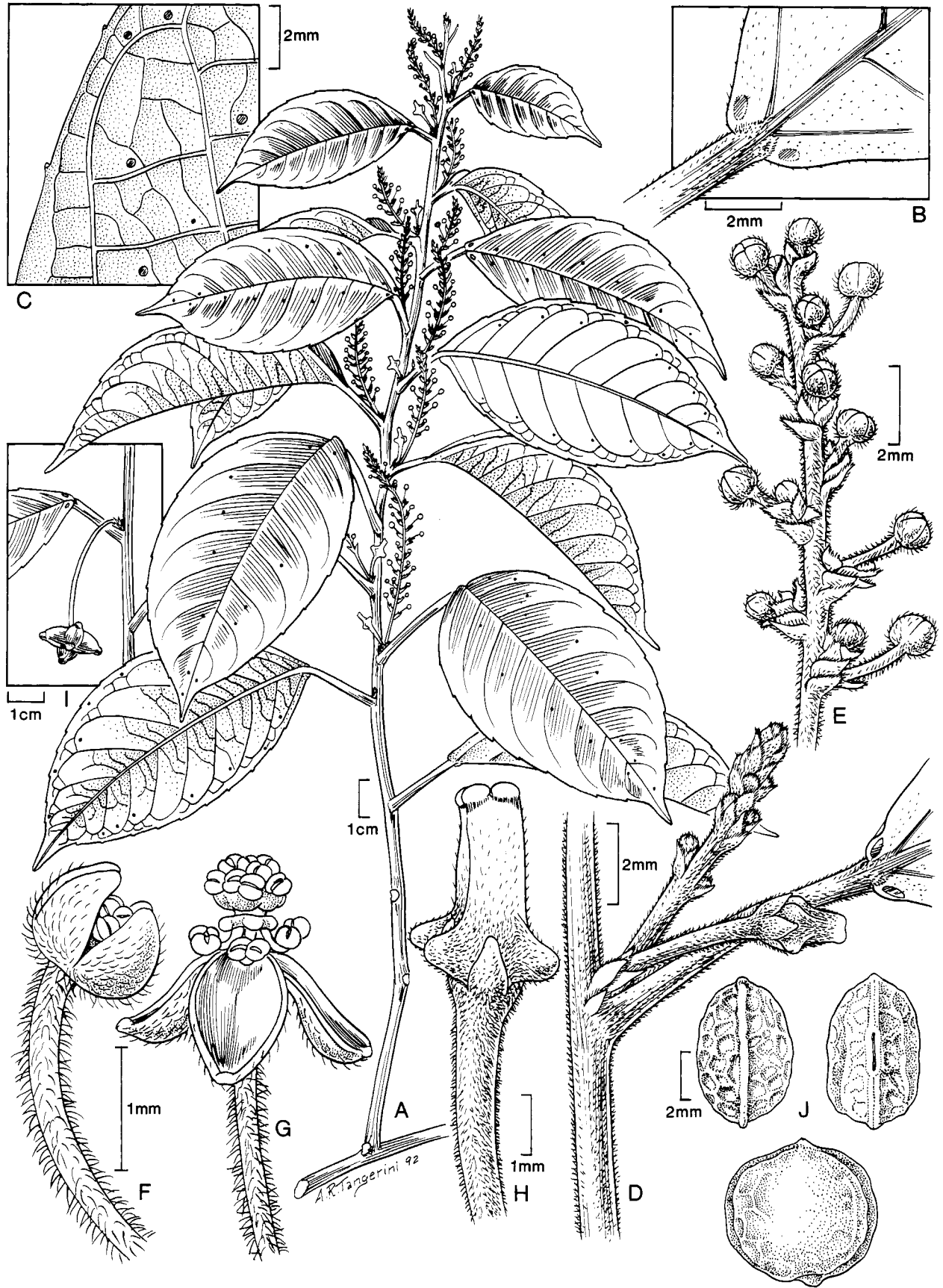


FIGURE 11 (left).—*Plukenetia supraglandulosa* L.J. Gillespie: A, habit; B, leaf blade base, adaxial surface, showing pair of basilaminar glands; C, leaf blade, abaxial surface, showing scattered laminar glands; D, young inflorescence in leaf axil, showing basal position of pistillate flower; E, upper part of inflorescence showing staminate flower buds in condensed cymes; F, staminate flower bud beginning to open; G, staminate flower at anthesis; 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).

horn-like tubercle. Seeds lenticular, circular to broadly elliptic in outline, 7–7.3 × 4.6–4.8 × 6.8–7.1 mm, reddish brown with raised reticulate pattern.

DISTRIBUTION.—Endemic to Surinam, French Guiana, and the Brazilian state of Amapá; five collections studied, of which one is from Surinam, three are from French Guiana, and one is from Amapá, Brazil.

ECOLOGY.—Occurs in submontane forest on lateritic plateau summits at 500–800 m in French Guiana. Flowers reported in January, August, and November; fruits reported in January and August.

SPECIMENS EXAMINED.—Surinam: Tumuc Humac Mts., Talouakem, 2°31'N, 54°45'W, *Acevedo 6022* (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).

#### 4. *Plukenetia verrucosa* Smith

FIGURE 12

*Plukenetia verrucosa* Smith, *Nova Acta Regiae Soc. Sci. Upsal.*, 6:4, 1799. [Type: Surinam, *Herb. Linnaeus* (holotype, LINN, microfiche IDC 5073.1489.2!).]

*Plukenetia integrifolia* Vahl, *Eclog. amer.*, 3:43, 1807. [Type: Guyana, "Demerari," *von Rohr s.n.* (holotype, C, photo, A!).]

DESCRIPTION.—Twining vine, monoecious. Stems slender, glabrescent to sparsely pubescent; young stems sparsely to densely pubescent. Petiole 1–3 cm long, slender, pubescent; blade chartaceous, ovate or oblong-ovate, 5–12 × 2–7 cm, apex long-acuminate with acumen 0.5–1.5 cm long, base cordate, truncate-cordate or truncate with broad, usually shallow sinus, sparsely pubescent on margin and veins above and below, 3-veined at base; basilaminar glands paired, subcircular to laterally elongate, 0.9–1.3 mm wide, with pair of stipels or small knob between; laminar glands circular, ~0.3 mm wide, adjacent to margin. Inflorescence axillary, terminal on short shoot 1–4 cm long, or terminal and appearing leaf-opposed, racemose, 0.5–4 cm long, axes tomentose; pistillate flower single at base, staminate flowers numerous in condensed cymes above; bracts triangular, 0.5–1 mm long, pubescent. Staminate pedicel 2–4.5 mm long, pubescent; bud globose, 1–1.4 mm in diameter; sepals 4, ovate, ~1 mm long, apex acute; annular disc between outer stamen whorl and inner anthers; androecium of 6–10 sessile anthers on a stout cylindrical receptacle and 4

outer stamens with filaments ~0.3 mm long. Pistillate pedicel 2–4.4 mm long, tomentose; sepals 4, lanceolate, ~1.5 mm long, pubescent; ovary deeply 4-lobed, ~1 × 2–2.5 mm, glabrous except for scattered hairs on lobes, lobes with prominent tubercle; style subglobose or obovoid, 1.5–2(–2.5) mm long and wide, glabrous, often with prominent 4-lobed stigmatic surface. Fruiting pedicel 0.8–1.5 cm long; capsule 4-lobed, ~6 × 11–14 mm, dehiscent, each carpel lobe prominently tuberculate. Seeds lenticular, subcircular in outline, ~6 × 4 × 5 mm, brownish gray with white markings, surface pitted.

DISTRIBUTION.—Guianas, Trinidad, and northern Amazonian Brazil (Amapá, northeast Amazonas, Pará, and Roraima); 14 collections studied, of which seven are from the Guianas (G:1, S:3, FG:3).

ECOLOGY.—Uncommon in disturbed areas or forest edge of lowland wet forest. Flowers reported in January, March, and July; fruits reported in January, July, and August.

SPECIMENS EXAMINED.—Guyana: Camp Macaw Falls, Waini R., *Beckett 8455* (BRG, NY). Surinam: Nickerie R., near Awawara, *BW 893* (K, U); Jodensavanne, *LBB 8565* (U); Voltzberg, *Pulle 221* (U). French Guiana: St. Jean du Maroni, *Benoist 893* (P); without specific locality, 1863, *Melinose* (?) (P); Karouany (or Maroni), *Sagot 22* (BM, G-BOIS, G-DC, K, MPU, P, U; consists of several collections).

#### 5. *Plukenetia volubilis* L.

FIGURE 10E

*Plukenetia volubilis* L., *Sp. pl.*, 1192, 1753. [Type: West Indies. Illustration t. 13 (lower half) in Plumier, *Nov. pl. amer.*, 47, 1703.]

*Plukenetia peruviana* Muell. Arg., *Linnaea*, 34:157, 1865. [Syntypes: Peru, *Herb. Pavon* (G-DC!, G!); Peru, "prov. Maynas," *Poeppig 2110* (not seen).]

*Plukenetia macrostyla* Ule, *Verh. Bot. Vereins Prov. Brandenburg*, 80, 1908. [Type: Brazil, Amazonas, Rio Juruá, bei Jaburú, *Ule 5864* (isotype, G!, fragment at F!).]

DESCRIPTION.—Twining vine or slender liana, monoecious. Stems glabrescent to pubescent; young stems pubescent. Petiole 2.5–7.5 cm long, glabrous to sparsely pubescent; blade chartaceous or membranous, triangular-ovate, 7–13(–18) × 4–10(–18) cm, apex long-acuminate with acumen 1–2 cm long, base truncate to cordate, glabrescent below, 3-veined at base; basilaminar glands paired, circular to laterally elongate, 1.5–3 mm wide, usually with small knob between; scattered laminar glands absent. Inflorescence axillary or terminal on short shoot, racemose, 5–18 cm long, axes sparsely to moderately pubescent; pistillate flower(s) 1 or rarely 2 at basal node(s), staminate flowers numerous in condensed cymes above; bracts narrowly triangular, 1.5–2.5 mm long. Staminate pedicel 2–3 mm long; bud subglobose, ~2 mm long, apex rounded to obtuse; sepals 4, ovate-elliptic, ~2 mm long, apex acute, glabrous; disc absent; stamens 20–25(–28) on convex receptacle; filaments ~0.5 mm long, dilated at base, attenuate at apex. Pistillate pedicel ~1.5 mm long; sepals 4, linear-triangular, 1.5–4 mm long, glabrous; ovary 4-winged, 1.5–2.5 × 3–5 mm, glabrous; style column elongate-cylindrical, 15–30

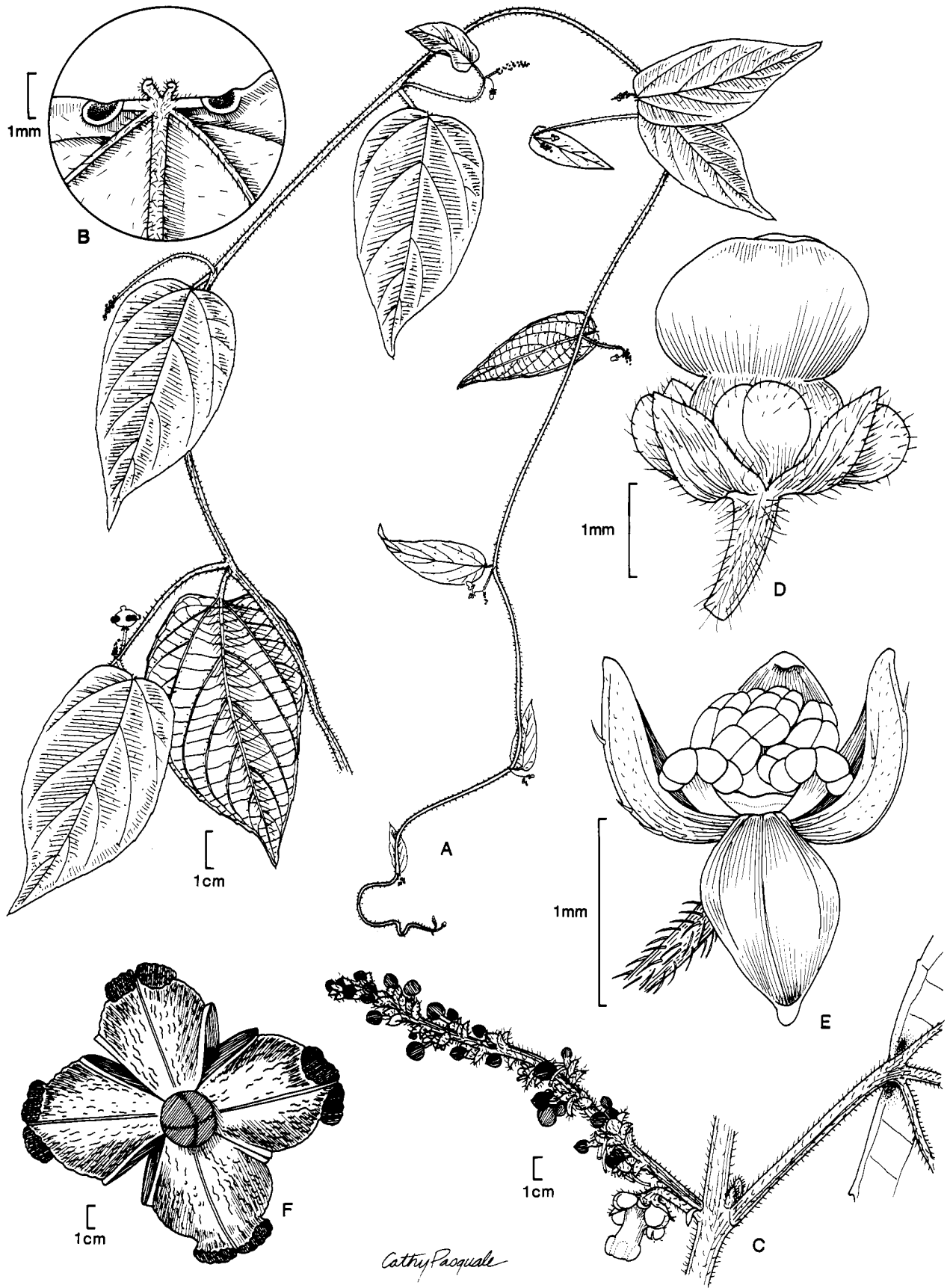




FIGURE 12 (left).—*Plukenetia verrucosa* Smith; A, habit; B, leaf blade base, adaxial surface, showing pair of basilaminar glands and pair of stipels; C, inflorescence, terminal but appearing leaf-opposed, with single basal pistillate flower; D, staminate flower showing two outer stamens having short filaments, an annular disc, and a central cluster of sessile anthers; E, pistillate flower; F, capsule, dried (A,B based on *Sagot 22*, P; C,D based on *Prance et al. 11255*, DAV; E based on *Irwin 48796*, US; F based on *Burchell 9369*, K).

× 0.7–1.5 mm, 4-lobed at apex, arms ~1 mm (rarely to 3 mm) long, often curled adaxially. Capsule deeply 4-lobed, 1.5–2.5 × 2.5–4(–6) cm, glabrous, initially fleshy, becoming woody and dehiscent, each carpel lobe with central wing to 2 mm wide. Seeds lenticular, broadly oblong in outline, 1.6–2 × 0.7–0.9 × 1.5–1.7 cm, brown with course dark brown markings.

DISTRIBUTION.—Widespread in the Lesser Antilles and South America, where it is found primarily in the northern and western regions and margins of the Amazon Basin in Surinam, Venezuela (Amazonas), Colombia (Meta), Ecuador, Peru, Bolivia, and Brazil (western Amazonas, Pará); 50 collections studied, of which two are from Surinam (S:2).

ECOLOGY.—Occurs in disturbed areas or forest edge of lowland moist or wet forest, below 900 m. In Surinam flowers reported in April and August, fruits in August and September.

SPECIMENS EXAMINED.—Surinam: West River, 2–5 km SW of Juliana Top, *Irwin et al. 54897* (F, GH, MO, NY, U, US); area of Kalalebo Dam project, *Lindeman et al. 636* (MO, U).

USES.—Vines are occasionally cultivated in western Amazonia for the seeds that apparently are edible when roasted (although seeds of wild plants were found to be distasteful and

inedible when eaten raw). Cultivated plants frequently have larger 5–6 carpelled fruit and more prominently serrate leaf margins (Gillespie, 1993b).

6. Genus *Tragia* L.

*Tragia* L., Sp. pl., 980, 1753. [Lectotype: *T. volubilis* L.]

DESCRIPTION.—Herbs, twining vines or subshrubs, monoecious or rarely dioecious. Stems and foliage usually covered with urticating hairs. Leaves simple, alternate, petiolate; stipules usually small, deciduous; blade pinnately or palmately veined, entire, lobed, or serrate; glands absent. Inflorescence a racemose or little branched paniculate thyrse, axillary, terminal on short shoots, or terminal but appearing leaf opposed, bisexual or rarely unisexual, with pistillate flower(s) basal; bracts small, triangular, eglandular. Staminate flowers pedicellate; sepals 3–6; corolla absent; disc intrastaminal and subtriangular or extrastaminal and segmented into filiform segments, often reduced or absent; stamens (1–)2–50; filaments present or anthers sessile; pistillode absent. Pistillate flowers pedicellate; sepals (3–)6; corolla absent; disc absent; ovary 3-locular, densely covered with urticating hairs; styles slender, partly connate. Fruit a 3-seeded capsule, 3-lobed, dehiscent, usually covered with urticating hairs. Seeds globose to ellipsoid, ecarunculate.

DISTRIBUTION.—About 130 species in tropical and subtropical regions of the New World, Africa, south and southwestern Asia, and Australia; four species are in the Guianas.

LITERATURE.—Pax and Hoffmann (1919a:32–101); Gillespie (1994b).

Key to the Species of *Tragia*

- 1. Inflorescence appearing dichotomous, consisting of staminate main axis to 18 cm long and a pistillate basal branch to 10 cm long; stamens 8–17; staminate disc segments present; fruit pedicel 1–4 mm long . . . . . 2
- Inflorescence racemose, to 10 cm long, with 1–2 pistillate flower(s) at the basal node(s); stamens 1–3; staminate disc segments absent; fruit pedicel 1–40 mm long . . . . . 3
- 2. Leaf blade palmately veined, base cordate; stamens 7–10; disc segments 6–7 . . . . . 1. *T. fendleri*
- Leaf blade pinnately veined, base acute or obtuse; stamens 14–17; disc segments 8–9 . . . . . 2. *T. lessertiana*
- 3. Glandular hairs present on stem, petioles, and inflorescence axes; inflorescence 4–9 cm long; fruit pedicel less than 0.5 cm long . . . . . 3. *T. tabulaemontana*
- Glandular hairs absent; inflorescence 1–4 cm long; fruit pedicel 1.5–4 cm long . . . . . 4. *T. volubilis*

1. *Tragia fendleri* Muell. Arg.

FIGURE 13A–D,G

*Tragia fendleri* Muell. Arg., *Linnaea*, 34:179, 1865. [Type: Venezuela, near Biscaine, *Fendler 1208* (holotype, G-DC!; isotypes, G!, G-DC!, GH!, MO!).] *Tragia japurensis* Muell. Arg. in *Mart.*, *Fl. bras.*, 11(2):404, 1874b. [Type:

Brazil, Alto Amazonas, Maribi, Japurensi District, *Martius s.n.* (holotype, M, photo F6626!).]

DESCRIPTION.—Twining vine, monoecious. Stems slender, covered with urticating hairs. Leaves covered with urticating hairs; petiole 2.5–11 cm long; blade chartaceous, elliptic, ovate

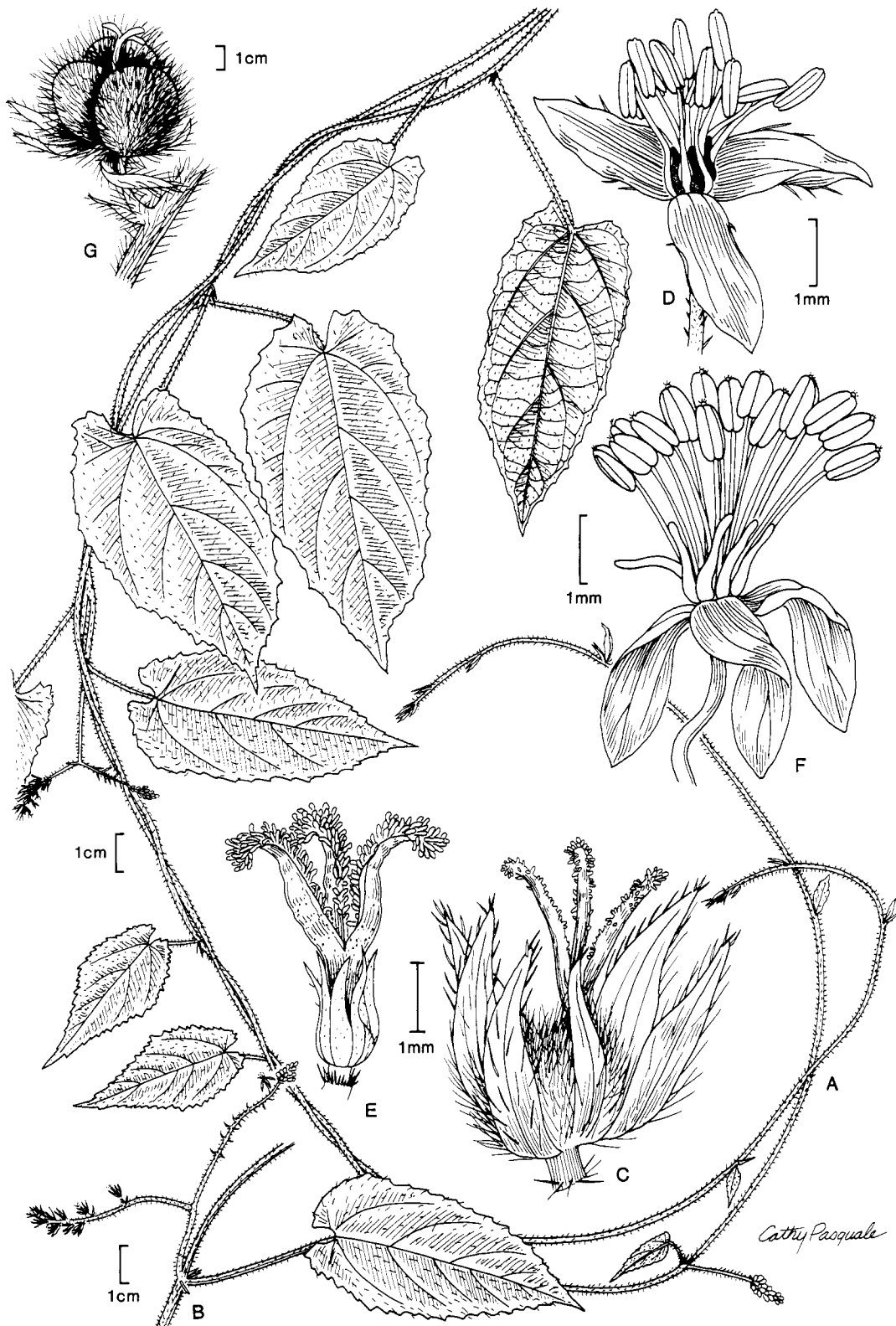


FIGURE 13.—*Tragia fendleri* Muell. Arg. and *Tragia lessertiana* (Baill.) Muell. Arg. A-D,G, *T. fendleri*: A, habit; B, inflorescence showing staminate main axis and pistillate branch at left; C, pistillate flower; D, staminate flower; G, capsule (A-D based on Gillespie et al. 1678, US; G based on Steyermark et al. 114589, MO); *T. lessertiana*: E, pistillate flower; F, staminate flower (E,F based on Webster 24119, DAV).

or oblong-ovate, 8–15.5 × 3.5–8.5 cm, margin dentate with teeth large and somewhat rounded, sometimes lobate near base, apex long-acuminate, base cordate, sinus angular, narrow to moderately broad, 0.6–1.6 cm deep, palmately veined with 5 basal veins. Inflorescence terminal, consisting of a staminate main axis with a single pistillate basal branch; peduncle 1–3 cm long, elongating in fruit to 6.5 cm; staminate axis racemose, 1.5–7 cm long; pistillate axis racemose, 2.5–7 cm long, elongating in fruit to 17 cm; bracts lanceolate, apex attenuate, staminate bracts ~2 mm long, pistillate bracts 3–4 mm long; flowers numerous, 1 per node; axes densely covered with urticating hairs. Staminate pedicel 2.0–3.5 mm long; bud obovoid, 2.0–2.6 mm long; sepals 3(–4), oblong elliptic or elliptic, ~2.5 mm long, apex acute; disc segments 6–7, slender, ligulate, 0.7–1 mm long, apex narrowed; stamens 7–10, outer whorl of 6(–7) alternating with and basally adnate to disc segments, inner cluster of 2–3; filaments slender, 1–1.5 mm long; anthers sagitate, ~1 mm long. Pistillate pedicel 0.3–0.5 mm long; sepals 6, lanceolate, 3–3.5 mm long; ovary globose, ~1 mm in diameter, very densely covered with urticating hairs; styles 3–3.5 mm long, connate one-third to one-half of length, inner surface papillate. Fruiting pedicel 1.5–4 mm long; sepals persistent, 5–8 mm long; capsule distinctly 3-lobed, 3–5 × 6–10 mm, densely covered with urticating hairs. Seeds globose or ellipsoid-globose, 3–3.5 mm long, pale brown with red-brown spots.

**DISTRIBUTION.**—Panama, Venezuela, Guyana, and Brazil (Amazonas); nine collections studied, of which two are from Guyana.

**ECOLOGY.**—Occurs in Guyana on white sand savanna or at the savanna/seasonal forest margin. In Guyana flowers reported between April and June; fruits reported in June.

**SPECIMENS EXAMINED.**—Guyana: Natun Bush Island, ~2 km SSW of Dadanawa, Rupununi Savannas, *Gillespie et al. 1678* (US); NW slopes of Kanuku Mts. in drainage of Moku-moku Creek, *Smith 3558* (A, F, NY, U, US).

## 2. *Tragia lessertiana* (Baill.) Muell. Arg.

FIGURE 13E,F

*Tragia lessertiana* (Baill.) Muell. Arg., *Linnaea*, 34:178, 1865.

*Bia lessertiana* Baill., *Étude Euphorb.*, 502, 1858. [Type: Brazil, *Herb. Delessert* (holotype, G!; fragments at F!, P!).]

**DESCRIPTION.**—Twining vine, monoecious. Stems slender, often woody, sparsely covered with urticating hairs. Petiole 1–5 cm long, sparsely covered with urticating hairs; blade chartaceous, oblanceolate or narrowly elliptic, 6–11.5 × 2–5.5 cm, margin serrate, apex acute or acuminate, base cuneate, acute or narrowly obtuse, sparsely covered with urticating hairs or glabrescent, pinnately veined. Inflorescence terminal, consisting of a staminate main axis with a single pistillate basal branch; staminate axis racemose, 5–20 cm long, with flowers

numerous, 1 per node; pistillate branch racemose, 3–10 cm long, elongating to 25 cm in fruit, flowers numerous, 1 per node; axes sparsely covered with urticating hairs; staminate bracts lanceolate, ~1 mm long; pistillate bracts lanceolate, 1.5–2 mm long, apex attenuate. Staminate pedicel 3–5 mm long; bud oblong-ellipsoid (or ovoid), 3–4 mm long, apex acute; sepals 3, narrowly oblong, 3–4 mm long, apex acute; disc segments 8–9, ligulate, 1.5–2.5 mm long, in whorl exterior to stamens; stamens 14–17, outer whorl of 8–9 alternating with and basally fused to disc segments, inner cluster of 6–9; filaments slender, 2–3.5 mm long; anthers sagitate, ~1 mm long. Pistillate pedicel ~0.5 mm long, jointed; sepals 6, lanceolate, ~1.5 mm long; ovary globose, ~0.5 mm in diameter, very densely covered with urticating hairs; styles 2.5–3 mm long, connate about one-quarter to one-half of length, usually slender, inner surface papillate. Fruiting pedicel 2–3 mm long; sepals persistent, 3–4 mm long; capsule 3-lobed, ~4.5 × 7 mm, sparsely covered with urticating hairs. Seeds ellipsoid-globose, ~3.5 mm long, pale brown with darker brown spots.

**DISTRIBUTION.**—The Guianas and Brazil (Amapá, Maranhão); 20 collections studied, of which 15 are from the Guianas (G:2, S:2, FG:11).

**ECOLOGY.**—Occurs in clearings or other disturbed areas of moist to wet forest. Flowers and fruits throughout the year.

**SELECTED SPECIMENS EXAMINED.**—Guyana: Mabura Hill, *Maas et al. 5910* (MO, NY, U); Mabura Hill, *Pipoly & Boyan 7573* (NY, US). Surinam: Nassau, *Lanjouw & Lindeman 2618* (U); Brownsberg Nature Preserve, *Webster 24119* (DAV, GH, MO, NY, U). French Guiana: Montagne de Kaw, *Feuillet 562* (CAY, U); Saül, *Granville 2783* (CAY, P, U, US); Saül, *Mori & Gracie 18414* (NY); Montagne de Kaw, *Hoff 5548* (CAY, U); S of airfield at Saül, *Skog et al. 7378* (CAY, NY, P, US).

**NOTES.**—The two collections from Guyana representing the westernmost population of the species differ from all other collections examined in their broader disc segments, ovoid (rather than oblong-ellipsoid) staminate buds, and thicker style branches.

## 3. *Tragia tabulaemontana* L.J. Gillespie

FIGURE 14

*Tragia tabulaemontana* L.J. Gillespie, *Novon*, 4:333, figs. 3, 4, 6, 8, 10, 1994b. [Type: French Guiana, Sommet Tabulaire, about 40 km SE de Saül, *Granville 3637* (holotype, US!; isotype, CAY!).]

**DESCRIPTION.**—Twining vine, monoecious. Stems slender; stems and petioles puberulous, sparsely to moderately hirsute, and with long-stipitate glandular hairs 0.5–1 mm long and urticating hairs 0.2–0.5 mm long. Petiole 0.8–3.2 cm long; blade thin-chartaceous, narrowly obovate or narrowly elliptic, 5–14 × 2–5.5 cm, margin serrate with serration apex obtuse and minutely glandular, apex acuminate, base narrowly cordate

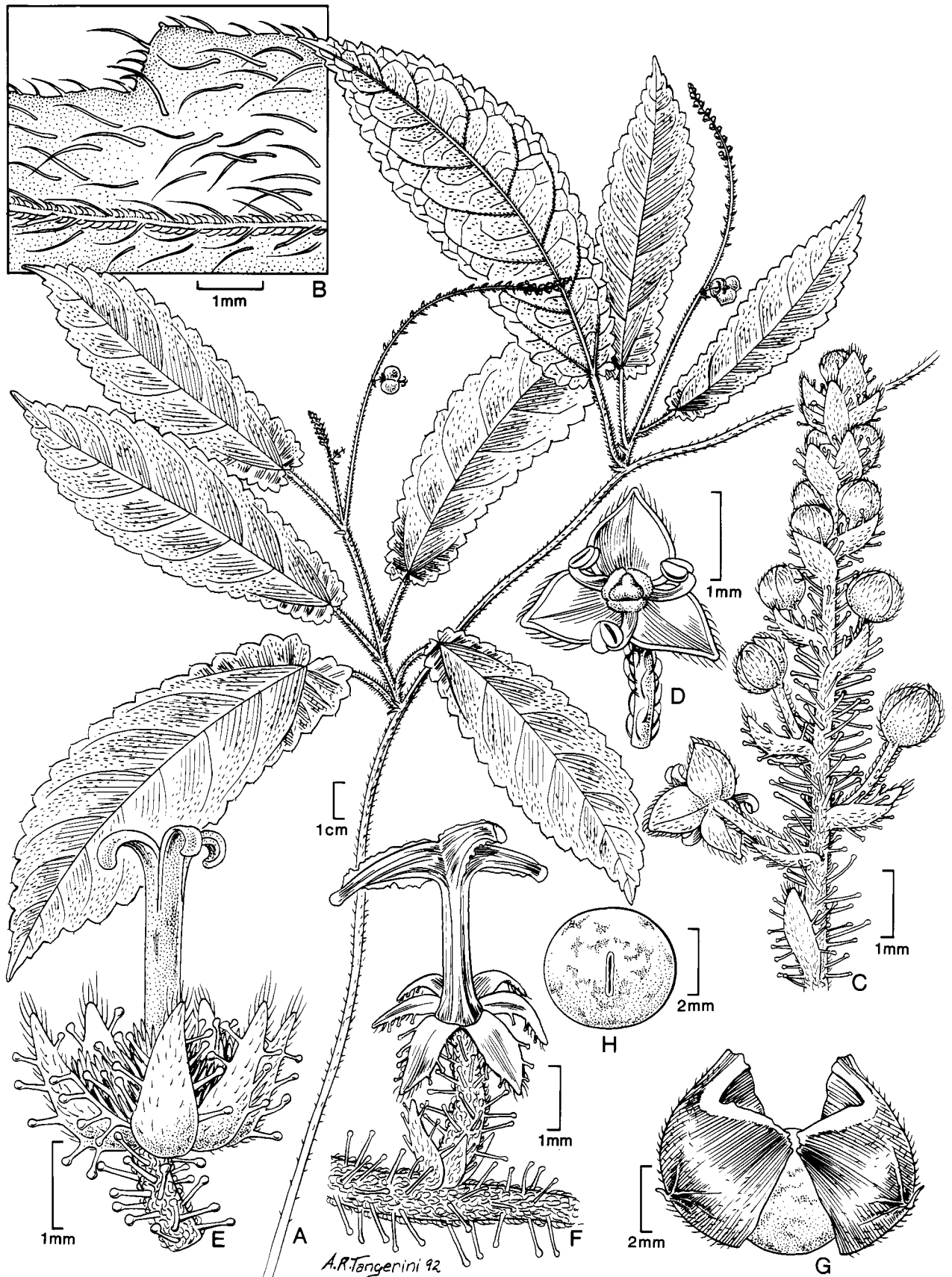


FIGURE 14 (left).—*Tragia tabulaemontana* L.J. Gillespie: A, habit; B, leaf blade, upper surface; C, upper part of inflorescence showing single open staminate flower with staminate buds above; D, staminate flower; E, pistillate flower; F, columella and persistent sepals on infructescence axis; G, mericarp of dehisced capsule with enclosed seed; H, seed, ventral view (A-E based on *Granville 3637*, US; F based on *Granville 3576*, CAY; G,H based on *Granville 3637*, CAY).

with sinus 2–6 mm deep, sparsely hirsute on both surfaces, venation pinnate, basal secondary vein pair diverging at a more acute angle than upper secondary veins. Inflorescence terminal on short shoots or appearing leaf-opposed, racemose, 4–9 cm long, axes puberulous with numerous long-stipitate glandular hairs and scattered short urticating hairs; single pistillate flower at basal node, staminate flowers numerous above, 1 per node; bracts narrowly triangular-ovate, 1–1.4 mm long. Staminate pedicel 1–1.7 mm long, puberulous; bud triangular-ovoid, ~1 mm long, apex obtuse; sepals 3, very broadly ovate, 1–1.2 mm long, sparsely hirsute particularly along margin and at apex; disc-like structure obtuse-triangular, intrastaminal, adnate to base of stamens; stamens 3, filaments 0.5–0.6 mm long, conical, slender at apex, highly dilated at base, anthers 0.2–0.3 mm long. Pistillate pedicel ~1 mm long, puberulous, hirsute at apex, with glandular hairs along margin; sepals 6, lanceolate, ~2 mm long, with urticating and glandular hairs; ovary 3-lobed, ~1 × 1.8 mm, densely covered with urticating and glandular hairs; styles 2.5–3.5 mm long, connate about two thirds of length, arms recurved. Fruiting pedicel 2–6 mm long; sepals persistent, reflexed; capsule 3-lobed, ~4.5 × 7–8 mm, sparsely covered with urticating hairs and sometimes glandular hairs; columella persistent with 3 perpendicular slender apical arms. Seeds subglobose, 3.8–4 mm in diameter, pale dull yellow with brownish markings.

DISTRIBUTION.—Known only from Sommet Tabulaire in French Guiana; two collections studied.

ECOLOGY.—Occurs in moist submontane forest on the southern and western slopes of Sommet Tabulaire, collections from 550–600 m. The two collections, both with flowers and fruits, were made in August.

SPECIMENS EXAMINED.—French Guiana: Sommet Tabulaire, ~50 km SE de Saül, *Granville 3576* (CAY, U, US).

#### 4. *Tragia volubilis* L.

*Tragia volubilis* L., Sp. pl., 980, 1753. [Type: Jamaica, Herb. Linnaeus (holotype, LINN, microfiche IDC 1103.1!).]

DESCRIPTION.—Twining vine, monoecious. Stems slender, becoming somewhat woody; stems and foliage sparsely to densely covered with urticating hairs. Petiole 0.5–1.5 cm long; stipules 2–3 mm long; blade chartaceous, narrowly triangular-ovate, 3–8 × 1–2.5 cm, margin serrate, apex acuminate, base truncate or truncate-cordate, 3-veined at base. Inflorescence axillary (Guiana specimens), terminal on short shoots or appearing leaf-opposed, racemose, 1–4 cm long, axes pubescent; single pistillate flower at basal node, staminate flowers numerous above, 1 per node; bracts narrowly ovate-triangular, 1–1.5 mm long. Staminate pedicel ~1 mm long, with urticating hairs; bud narrowly ellipsoid, 0.8–1 mm long, apex broadly acute; sepals 3, ovate, ~1 mm long, apex acute, glabrous except at base; disc absent; stamens 1–3, filaments 0.2–0.3 mm long and wide, anthers ~0.3 mm long. Pistillate pedicel ~1.5 mm long, very densely pubescent; sepals 6, ovate, ~1.5 mm long, apex acute, glabrescent or sparsely pubescent; ovary 3-lobed, ~1 mm in diameter, very densely covered with urticating hairs; styles ~1 mm long, connate one-half of length, arms divergent. Fruiting pedicel 1.5–4 cm long, pubescent; sepals persistent, ~2 mm long; capsule 3-lobed, 3–3.5 × 5.5–6.5 mm, pale brown with dark brown markings, covered with urticating hairs; columella persistent, slender with expanded 3-pointed apex. Seeds ellipsoid-globose, ~3 mm long, pale with reddish brown markings.

DISTRIBUTION.—Widespread in the Neotropics from Guatemala and the West Indies to Bolivia, Argentina, and Brazil, apparently absent from the central Amazon Basin, introduced in Africa; 50 collections studied, of which 18 are from the Guianas (S:1, FG:17).

ECOLOGY.—A weed of open and disturbed areas, found along the coast in Surinam and French Guiana.

SELECTED SPECIMENS EXAMINED.—Surinam: Bergendane Majo, *Foche 1027* (U). French Guiana: vicinity of Cayenne, *Broadway 51* (NY, US); Ile de Cayenne, *Prévost 1492* (CAY); Cayenne, *Rothery 75* (NY).

## Appendix 1

### Numerical List of Accepted Taxa

1. *Omphalea* L.
  - 1-1. *Omphalea diandra* L.
2. *Pera* Mutis
  - 2-1. *Pera bicolor* (Klotzsch) Muell. Arg.
  - 2-2. *Pera decipiens* (Muell. Arg.) Muell. Arg.
  - 2-3. *Pera glabrata* (Schott) Baill.
3. *Dalechampia* L.
  - 3-1. *Dalechampia affinis* Muell Arg.
  - 3-2. *Dalechampia attenuistylus* Armbruster
  - 3-3. *Dalechampia brevicolumna* Armbruster
  - 3-4. *Dalechampia brownsbergensis* Webster & Armbruster
  - 3-5. *Dalechampia dioscoreifolia* Poepp.
  - 3-6. *Dalechampia fragrans* Armbruster
  - 3-7. *Dalechampia heterobracteata* Armbruster
  - 3-8. *Dalechampia magnoliifolia* Muell. Arg.
  - 3-9. *Dalechampia megacarpa* Armbruster
  - 3-10. *Dalechampia micrantha* Poepp.
  - 3-11. *Dalechampia olympiana* Kuhlman & Rodrigues
  - 3-12. *Dalechampia papillistigma* Armbruster
  - 3-13. *Dalechampia parvibracteata* Lanj.
  - 3-14. *Dalechampia scandens* L.
    - 3-14a. *Dalechampia scandens* var. *scandens*
    - 3-14b. *Dalechampia scandens* var. *fallax* Muell. Arg.
  - 3-15. *Dalechampia stipulacea* Muell. Arg.
  - 3-16. *Dalechampia tiliifolia* Lam.
  - 3-17. *Dalechampia* aff. *cissifolia* Poepp.
  - 3-18. *Dalechampia* aff. *triphyllo* Lam.
4. *Haematostemon* (Muell. Arg.) Pax & K. Hoffm.
  - 4-1. *Haematostemon guianensis* Sandwith
5. *Plukenetia* L.
  - 5-1. *Plukenetia loretensis* Ule
  - 5-2. *Plukenetia polyadenia* Muell. Arg.
  - 5-3. *Plukenetia supraglandulosa* L. J. Gillespie
  - 5-4. *Plukenetia verrucosa* Smith
  - 5-5. *Plukenetia volubilis* L.
6. *Tragia* L.
  - 6-1. *Tragia fendleri* Muell. Arg.
  - 6-2. *Tragia lessertiana* (Baill.) Muell. Arg.
  - 6-3. *Tragia tabulaemontana* L. J. Gillespie
  - 6-4. *Tragia volubilis* L.

## Appendix 2

### Collections Studied

(Numbers in parentheses following collection numbers refer to species numbers in taxonomic treatments and in Appendix 1)

#### Guyana

Atkinson, D.J., 114 (4-1)  
 Beckett, J.E., 8455 (5-4)  
 Beckett & Kortright, 8640 (5-2)  
 Boom, B.M., 7117 (2-3)  
 Boom & Gopaul, 7326 (2-1)  
 Boyan, R., 39 = FD 7863 (2-1)  
 Cook, C.D.K., 44 (3-13b)  
 Cruz, J.S. de la, 3186 (1-1)  
 Davis, T.A.W., 113 = FD 2104 (2-3); 238 = FD 2229 (2-1); 385 = FD 2381 (2-3); 40 = FD 2812 (2-1)  
 Ek et al., 1187 (3-11)  
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(Synonyms are in italics)

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    *lessertiana* (Baill.) Muell. Arg.
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- Dalechampia L.  
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    aff. *triphylla* Lam.  
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    *attenuistylus* Armbruster  
    *brevicolumna* Armbruster  
    *brevipes* Briquet  
    *brownsbergensis* Webster & Armbruster  
    *cissifolia* Poepp.  
    *diocoreifolia* Poepp.  
    *fragrans* Armbruster  
    *guianensis* Klotzsch  
    *heterobracteata* Armbruster  
    *heterophylla* Vahl  
    *magnoliifolia* Muell. Arg.  
    *megacarpa* Armbruster  
    *micrantha* Poepp.  
    *mollis* Vahl  
    *olympiana*  
    *papillistigma* Armbruster  
    *parvibracteata* Lanj.
- peruviana* Lam.  
    *pruriens* Griseb.  
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    *rubiformis* Spreng.  
    *ruboides* H.B.K.  
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    *scandens* var. *fallax* Muell. Arg.  
    *sidaefolia* H.B.K.  
    *spathulata* var. *amazonica* (Ule) Pax and Hoffmann  
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    *triphylla* Lam.
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    *abutifolia* Ducke  
    *polyadenia* (Muell. Arg.) Ducke  
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    *decipiens* (Muell. Arg.) Muell. Arg.
- distichophylla* (Mart.) Baill.  
    *ferruginea* (Schott) Muell. Arg.  
    *glabrata* (Schott) Baill.  
    *nitida* (Benth.) Jabl.  
    *tomentosa* (Benth.) Muell. Arg.
- Peridium*  
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    *bicolor* var. *tomentosum* Benth.  
    *decipiens* Muell. Arg.  
    *ferrugineum* Schott  
    *glabratum* Schott  
    *schomburgkianum* Benth.
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    *macrostyla* Ule  
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    *polyadenia* Muell. Arg.  
    *supraglandulosa* L.J. Gillespie  
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    *volubilis* L.
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- Tragia L.  
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    *japurensis* Muell. Arg.  
    *lessertiana* (Baill.) Muell. Arg.  
    *tabulaemontana* L.J. Gillespie  
    *volubilis* L.

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hachiballi

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hatsiballi koelnoe  
idaballie  
kamua-tan  
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palaramauloeloe  
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