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SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF SIPARUNA (MONIMIACEAE) IN PANAMA

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SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF SIPARUNA (MONIMIACEAE) IN PANAMA

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SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF

SIPARUNA (MONIMIACEAE) IN PANAMA

APPROVED BY

DISSERTATION COMMITTEE

PREFACE

This dissertation is prepared as three separate manuscripts with independent table and figure numeration in accordance with the format of refereed journals. The first article, "A Revision of Panamanian Species of Siparuna (Monimiaceae)," is in the format of The Annals of the Missouri Botanical Garden. The second article, "Phenological and Spatial Relationships Among Three Dioecious Species of Siparuna (Monimiaceae) in Panama," is in the format of Biotropica. The third article, "Composition of Essential Oil from the Leaves of Siparuna guianensis," is in the format of Planta Medica. Citations to Antonio (1983) refer to this dissertation.

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SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF <u>SIPARUNA</u> (MONIMIACEAE) IN PANAMA

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ABSTRACT

This study involves a taxonomic treatment of the species of Siparuna (Monimiaceae) found in Panama. Included are keys, descriptions, distributions, and photographs. Currently there are 16 species of Siparuna in Panama. Six of these are described as new species previously unknown. A taxonomic interpretation of these taxa were based upon extensive field study and analysis of herbarium specimens. Floral characters proved to be very important taxonomically, especially when viewed by the light and scanning electron microscopes.

The dioecious species, Siparuna pauciflora, S. nicaraguensis, and S. vinosa occur sympatrically in the premontane wet forests of Panama. The two tree species, S. pauciflora and S. nicaraguensis, have seasonal patterns of flowering and fruiting with flowering coincident with the end of the dry season and fruiting peak at the beginning of the rainy season. Siparuna vinosa, a shrub, is aseasonal in both flowering and fruiting. No patterns of spatial segregation were observed in S. pauciflora or S. nicaraguensis; however, S. vinosa tended to be

aggregated. Plants such as S. vinosa with few flowers may increase the probability of seed set by flowering over a longer period of time and also occurring in aggregate. A longer fruiting period also increases the probability of seed dispersal.

Some components of the essential oil from the leaves of Siparuna guianensis (Monimiaceae) were identified and determined in the steam-volatile extract. The major constituents are curzerenone (26%) and curzerenone types (42%), as well as myristicin or an isomer (8%). This represents the first chemical study of the composition of Siparuna guianensis oil.

A REVISION OF PANAMANIAN SPECIES OF *SIPARUNA* (MONIMIACEAE)

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Monimiaceae sensu lato is a diverse assemblage of some 34 genera and over 350 species. The family is almost entirely tropical or subtropical in its distribution, especially in the Southern Hemisphere (Hutchinson, 1964).

Jussieu first described the family in 1809 (as Monimieae). At that time the family consisted of three genera Monimia Thouars, Atherosperma Labill., and Siparuna Aubl. (Citrosma Ruiz. & Pav.). Since that time, the family has undergone considerable taxonomic flux. A comparison of different orders in which Monimiaceae have been placed is given in Table 1. Cronquist (1981) believed Monimiaceae to be critical to an understanding of Laurales. He pointed out that a search for relatives of each of the other families in the order usually leads into one or another part of the Monimiaceae.

Part of the explanation for ordinal shifts in Monimiaceae lies in the circumscription of the family itself. Following Jussieu, a number of genera were added to the family with the subsequent naming of tribes within Monimiaceae (Table 2). This early trend of tribal divisions has today been replaced with the creation of subfamilies within Monimiaceae. Even more recently, Schodde (1970) officially proposed family status for these once subfamilial divisions. Currently there are four generally recognized subfamilies of Monimiaceae (Moimioideae, Atherospermatoideae, Hortonioideae, Siparunoideae).

The largest genus in Monimiaceae is Siparuna. Siparunoideae, of which Siparuna is a member, is characterized by bisporangiate valvate stamens, erect basal ovules, a single nodal trace and a basic chromosome number of x=22. Also having these features are Atherospermoideae, and the two groups probably represent lines of parallel evolution from a common ancestral stock (Schodde, 1970). Lacking in the Siparunoideae are the basal staminal appendages, septate wood fibers and hippocrepiform sclerids of the Atherospermoideae. Advanced trends such as vessels with simple perforation plates, and closed, reduced, floral receptacles with a velum replacing the perianth occur in Siparunoideae. The subfamily also has inaperturate, granulate pollen, and bird-dispersed carpels. Three genera comprise the subfamily: Bracteanthus with a single species in Brazil; Glossocalyx with three species in west tropical Africa; and Siparuna with over 150 species in tropical America.

Morphologically Monimiaceae have been studied extensively (Endress, 1972, 1973, 1980a; Money et al. 1950; Lemesle & Prichard, 1954; Sampson, 1969). As regards floral morphology, Monimiaceae are coherent yet at the same time diverse. Many genera exhibit trends toward floral specialization. These following evolutionary trends were summarized by Endress (1980b).

1) Reduction in the size of the tepals.
2) Size of entrance to floral cups reduced.
3) Enclosure of the inner tepals in the floral cup.
4) Ovaries enclosed in the floral cup.
5) Carpels or ovaries permanently enclosed, dehiscence only in fruit of the cup.
6) Ovaries embedded in wall of the floral cup.
7) Stamens enclosed in the floral cup of the staminate flower.
8) Anther slits confluent at the apex.

Heywood (1978) stated that the structure of the monimiaceous flower suggests magnolia-like flowers with a concave floral axis, the stamen and carpels depressed within the axis. Within the family, Siparuna flowers are less specialized than most in the family and are similar to those of Palmeria and Monimia.

Flowers of the Panamanian species of Siparuna have well developed floral cups as in S. tonduziana (Fig. 1) and S. pauciflora (Fig. 2). The majority of the species have inconspicuous tepals such as those in S. vinosa (Fig. 3) but in S. nicaraguensis they can be quite conspicuous (Fig. 4). In pistillate flowers the styles are long and protrude out of the narrow apical pore (Fig. 5) as in S. nicaraguensis. The floral roof in Siparuna upon which the diaphragm aperture-like pore is located is called the "velum". The individual carpels are positioned in the wall of the hypanthium and are free with broad bases as shown in S. pauciflora (Fig. 6).

Staminate flowers of species of Siparuna are generally of very similar size and shape to the pistillate. Stamens can vary anywhere from approximately 10-12 in S. pauciflora (Fig. 7) to a more representative number of 6 in S. nicaraguensis (Fig. 8). The anthers are two-locular (Fig. 9). Although said to open by two separate valves (Perkins & Gilg, 1901; Schodde, 1970), I agree with Endress (1980b) that the two valves are more or less confluent (Fig. 10). The valve, thus looks like a single apical opening. Unlike the pistillate flowers, the stamens are not embedded in the reticulum-like growth of the inner surface of the floral cup (Fig. 11).

In Siparuna the ripening carpels remain enclosed by the enlarging floral cup. When mature, the floral cup splits open as in S. darienensis (Fig. 12). Therefore, the floral cup and carpels functionally behave like the ovary wall and the seeds of a syncarpous gynoecium (Endress, 1980b). The carpels bear fleshy, brightly colored outgrowths, resembling arillate seeds (Endress, 1973).

Perkins (1901) published the first and only monograph of the genus Siparuna which was followed by a monograph of the family (Perkins, 1911). Since that time, virtually nothing has been done on the genus Siparuna from a taxonomic perspective. Treatments of the family in floras: Flora of Peru (Macbride, 1938); Flora of Costa Rica (Standley, 1937); and Flora of Panama (Duke, 1962) have raised the number of known species to over 150.

Siparuna is neotropical in its distribution, occurring from Mexico south through tropical South America. The genus was first described from French Guiana and the greatest development of species is in South America. No study has been made of the genus since Perkins (1901) treatment. The only key to the species remains that published by Perkins. The need for a revision of the entire genus is great, and it is hoped that a revision of the Panamanian species will ultimately lead to a monograph of the entire genus.

SIPARUNA

Siparuna Aubl., Hist. Pl. Guiane Fr. 2:864. June 1775. TYPE: S. guianensis Aublet.

Citrosma Ruiz & Pavon, Fl. Per. & Chil. Prodr. 134. Oct 1794

Leonia Mutis, ex Kunth, Synops. Pl. 1:462. 1822

Conuleum L.C. Richard ex A. Richard, Mem. Soc. Hist. Nat. Paris 1:391. 1823

Citriosma Tulasne, Ann. Sci. Nat. Bot. ser.4.3:32. May 1855 (orth. var.)

Angelina Pohl ex Tul., Arch. Mus. Nat. Par. 8:363. 1855 loc.cit.

Trees or shrubs from 1 to 7 m, rarely lianas; dioecious or monoecious; characterized by strong aromatic lemon-like odor. Leaves mostly opposite, sometimes ternate, rarely verticillate, membranaceous to pergameneous to coriaceous; margin subentire, entire or more often serrate, teeth often with an opaque, non-deciduous glandular cap with an acute apex; tooth shape generally acuminate-convex; venation with a secondary or tertiary entering the tooth medially and not joined by lateral veins; petioles often unequal, canaliculate; leaf base variable, rounded to obtuse, cordate to lobate to auriculate, rarely forming domatia; leaf apex acuminate to acute, cuneate to cuspidate; pubescence often of branched hairs, glabrous to densely hairy, the hairs simple or stellate, sometimes peltate-stellate scales, also tufts of unicellular trichomes; stomatal complexes anomocytic; venation brochidodromous. Inflorescence in axillary cymes, or sometimes paniculate or racemose. Flowers imperfect, small pedicellate to subsessile; receptacle usually campanulate, globose or urceolate; pistillate flowers

5 to 20 per inflorescence, 4-20 mm in diameter, petals 4-7, small and inconspicuous, sometimes obsolete, united below to form an annulus interior to which if often a flat or hemispherical, apically perforate velum; styles filiform or ligulate, free or connate at the base, often exserted from narrow apical pore; carpels 4 to many; ovule 1 in each carpel, basal, erect; staminate flowers 5 to 30 per inflorescence, 3-15 mm in diameter; stamens 1 to many, often unequal, arrangement scattered or circular; filaments ligulate to cylindric, often dilated or conduplicate; anthers oblong, two-locular, dehiscent by valves on the inner side. Fruit drupaceous or coriaceous, globose or obconic, permanently enclosed in the accrescent hypanthium; hypanthium wall forming pericarp. Seeds ascending, with copious endosperm, tuberculate, fleshy outgrowth on seeds often bright red, ultimately exposed by the irregular bursting of the aggregate fruit.

KEY TO THE SPECIES OF SIPARUNA IN PANAMA

a. Vines or lianas.................................. 13. S. sytsmania

aa. Trees or shrubs.

b. Monoecious; flowers globose, velum absent; seeds typically larger than 5 mm long, surface completely covered with arillate structure; petioles less than 1 cm in length.

c. Leaves elliptic to ovate, 2-5 cm wide, dense yellow stellate peltate scales, lateral veins parallel to slightly arched; flowers in pseudoumbels, petioles 4-5 mm long, stamens hippocrepiform ....1. S. crassiflora

cc. Leaves narrow oblong to elliptic, 3.5-9 cm wide, pubescence stellate to simple appressed hairs, lateral veins arched; flowers in cymes, petioles 5-9 mm long, stamens dilated .... 7. S. guianensis

bb. Dioecious; flowers disk-shaped, or if not, at least not globose; seeds 5 mm long or slightly smaller, surface incompletely covered by two lateral lobes; petioles greater than 1 cm in length.

d. Leaf margin irregularly strongly dentate, hairs stellate or simple usually over 0.8 mm long; pistillate flowers 1 cm or larger in diameter, tepals 2-4 mm triangular; fruits reniform to globose.

e. Leaf base cuneate to acute with exaggerated serrations at the base of leaf which appear as fringed appendages, leaves 13-29 cm long, 7-15 cm wide............. 6. S. fimbriata

ee. Leaf base cordate to nearly auriculate or rounded, leaves 16-48 cm long, 9-27 cm wide.

dd. Leaf margin entire, undulate or minutely denticulate, hairs stellate or simple less than 0.8 mm long; pistillate flowers less than 1 cm in diameter, tepal lobes rounded usually less than 2 mm in length; fruits typically globose.

f. Hairs simple and stellate to 0.8 mm long, leaf surface rough to touch..... .... 5. S. dressleriana ff. Hairs dense wooly to 2.5 mm long, hairs extending over margin by as much as 1.3 mm, lower leaf surface smooth to touch .... 15. S. tonduziana

g. Leaves mostly 2.5-5 cm wide, length rarely exceeding 14 cm, membranaecous.

h. Leaves entire or slightly denticulate.

i. Staminate flowers 1.5 mm in diameter, stamens 2 .... 3. S. diandra

ii. Staminate flowers 4-5 mm in diameter, stamens 6 .... 16. S. vinosa

hh. Leaves serrate, often the apical termination on the monimiod tooth is cassidate........... 11. S. riparia

gg. Leaves mostly over 5 cm in width, leaves often exceeding 14 cm in length, coriaceous.

j. Leaves, at least the lower surface, densely tomentose to nearly woolly.

k. Leaves 3.5-7 cm wide, never exceeding 22 cm in length, thick up to 1 mm........ 9. S. patelliformis

kk. Leaves 7-16 cm wide, frequently exceeding 35 cm in length, less than 1 mm thick.

l. Leaves wide, elliptic to obovate; tree, 2-7 m tall; flower pedicels 2-10 mm, stamens 10-30, petioles green ....10. S. pauciflora

ll. Leaves narrow, elliptic to elliptic; shrub or treelet, 1-3 m tall; flowers nearly sessile, stamens 4-6, petioles reddish .... 12. S. rosicosta

jj. Leaves, at least lower surface, sparcely pubescent.

m. Leaf base auriculate with prominent domatia .... 4. S. domatiata

mm. Leaf base cuneate to cuneate rounded.

n. Stems and branches with prominent lenticels .... 2. S. darienensis

nn. Stems and branches without prominent lenticels.

o. Upper leaf surface sparcely pubescent with simple and branched hairs; margin undulate denticulate; tepals 6; stamens 5-8, the exterior in a whorl or often connate .... 14. *S. tetraceroides*

oo. Upper leaf surface glabrous to sparsely stellate pubescent; margin mostly entire; tepals usually 4; stamens 6 outer 4 not connate .... 8. *S. nicaraguensis*

1. Siparuna crassiflora Perk., Engl. Bot. Jahrb. 28:702. p. 12. 1901. TYPE: Peru, Spruce 4907 (C, holotype).

Siparuna cuspidata A.DC. in DC., Prodr. XVI. 2. p. 655, 1868.

Citriosma myristicoides Spruce, Journ. Linn. Soc. V. 1861.

Shrub or tree 2-6 m tall; monoecious; aromatic; stems and branches terete, frequently covered with dense yellowish stellate peltate scales. Leaves opposite, narrow oblong to oblong to elliptic, membranaceous, 7-13.5 cm long, 2.3-5 cm wide; entire; apically long narrowly acuminate; base rounded to obtuse; often with numerous parallel lateral veins, more prominent on lower surface than upper, veins appear undulate on leaf surface; pubescence often of dense yellowish stellate peltate scales, upper leaf surface glabrous to sparsely pubescent minute scales, lower surface with more scales; petioles 4-5 mm long, opposing nearly always the same length. Inflorescence of 5-15 flowers, pseudo-umbels, ca. 1.5 cm long; pedicels 3-5 mm long; peduncles to 12 mm long; exterior of floral receptacle sparsely to densely covered with yellowish stellate peltate scales. Flowers yellowish-green to green with red tinge; receptacles subglobose; 2-3 mm in diameter; velum obsolete to an emarginate annulus; tepals obsolete; apical pore 1.5 mm in diameter, ruptured margins; styles several, 1-1.5 mm long, sometimes connate at bse, stamens typically 6, hippocrepiform, 1 mm wide, embedded in receptacle wall. Aggregate fruit ecallose, subglobose, 1 cm in diameter, not capped by persistent annulus, apical pore is barely closed. Seeds 8 mm long, few per fruit, thin arillate structure completely covers the surface, seed coat ornamented with distinct projections.

This species flowers from January to May and had been collected in fruit during August and September. Siparuna crassiflora differs significantly from all other species of Siparuna in Panama. The leaves with the unique vein pattern, a pseudo-umbel inflorescence, abundance of scales, paucity of seeds per fruit, somewhat hippocrepiform stamens, and the persistence of the apical pore open into fruit are all characters unique to this species of Siparuna. Further analysis of this species is needed along with a reevaluation of the generic boundaries in Monimiaceae before a decision is reached on whether or not to retain this species in Siparuna.

COLON: Near Agua Clara rainfall station, Santa Rita Ridge, Foster 1723 (DUKE, F). Santa Rita Ridge Road ca. 8.5 km from Boyd-Roosevelt Hwy., Mori & Kallunki 2071 (US). DARIEN: Cerro Pirre, Narciso Bristan 1232 (NY). Cloud forest, Cerro Campamento, S. of Cerro Pirre, Duke 15703 (US). PANAMA: El Llano-Carti Rd. 12 km from Pan-Am. Highway, 330-370 m, Gentry & Mori 14208 (PMS,US). 12-16 km above Pan-Am. Highway on road from El Llano to Carti-Tupile, 150-400 m, Kennedy 3142 (US). Along El Llano Carti-Tupile Rd. 12 mi above Pan-Am. Highway, Liesner 1162 (C, DUKE, F, K, NY, US). Along El Llano Carti-Tupile Rd. 12 mi above Pan-Am. Highway, 200-500 m, Liesner 1227 (NY, PMA, US). El Llano-Carti Rd. ca. 14 km N of Pan-Am. Highway, at El Llano, 450 m, Nee & Dressler 9336 (US, NY). VERAGUAS: 5 mi NW of Santa Fe on slope above Rio Primero Brazo, 700-1200 m, Croat 23116 (US).

2. Siparuna darienensis Duke ex T. Antonio, TYPE: PANAMA: Province of Darien, Along the Sambu River, southern Darien above tide limit, Pittier

5553 (US, holotype; NY, F, isotype). Fig. 13, 14, 15, 16.

Arbor dioecus 3-7 m altus, ramulis teretibus, pilis stellato, lenticellis conspicuus; folia opposita, elliptica vel angusta ovata, 12-24 cm longa, 6-12 cm lata; integra vel denticulata; apice acuminata; basi cuneata; petiolo 2.5-8.5 cm longo. Inflorescentiae feminea in axillis foliorum. Flores receptaculo 4 mm in diametro tepalis obsoletus; stylus ad 17. Inflorescentiae masculae in axillis foliorum. Flores viridis vel luteus, staminibut 6.

Tree 3-7 m tall; dioecious; aromatic; seldom branching from base; stems and branches terete; sparsely covered with minute stellate hairs, 0.2 mm long; conspicuous lenticels 0.8 mm long, 0.2 mm wide. Leaves opposite, elliptic to narrow obovate, membranaceous, 12-24 cm long, 6-12 cm wide; entire to rarely denticulate; apex acuminate; base cuneate; 7-9 pairs of lateral veins; pubescence rarely absent, sparse to moderate minute stellate hairs on upper and lower leaf surfaces; petioles 2.5-8.5 cm long, moderately to densely covered with minute stellate hairs, opposing sometimes differing in their lengths, without the distinct curvature of other species of *Siparuna* more or less uniform in thickness from stem to leaf base. Pistillate inflorescence of 5-15 flowers in axillary cymes, 1-3 cm long; pedicels 4-6 mm long. Flowers pale yellow to green; pubescence stellate over much of the receptacle, usually absent on velum; well developed receptacle; 4 mm in diameter; velum planar to rounded with the margins reflexed toward base of receptacle; tepals obsolete to minute, 4-5 lobes; apical pore 1 mm in diameter; styles up to 17, united at their middle, barely exserted beyond velum surface. Staminate inflorescence of 5-20 flowers; similar in size and shape to pistillate, although often more numerous; stamens 6, separate, 1 mm long, anthers valvate, minute, introrse. Aggregate fruits ecallose, globose, 1-1.5 cm in diameter, pale green to pink, bursting irregularly exposing a white to pink interior with up to 19 tuberculate seeds. Seeds 5 mm long, gray with black splotches, arillate structure covers the ovary with two lateral lobes and is bright red, surface somewhat ornamented.

This species is known at present only from the Darien and is easily recognized by the prominent lenticels (Fig. 14) on the stems and branches. The flowers are also distinctive in that the velum is reflexed toward the receptacle (Fig. 16). Siparuna darienensis flowers from December to April and is in fruit in April. The foliage is said to have a disagreeable odor.

DARIEN: North Punta Guayabo Grande, trail to top of ridge, 300-900 ft., Antonio 4277 (MO, F, NY, GH). Vicinity of Cerro Pirre, this side near the headwaters of Uruseca, Antonio 5325 (MO, F, NY, GH). Rio Sambu 0.5 mi above Rio Venado, Duke 9297 (US). Cerro Campamento, S of Cerro Pirre, Duke 15587 (NY). Vicinity of San Jose River, Duke & Bristan 403 (US). 0-2 mi E of Tres Bocas along the headwaters of Rio Cuasi, Kirkbride & Duke 1183 (NY). Vicinity of Cana, 1750 ft, Stern 468 (GH, US). Paca below Cana, Williams 718 (NY, US).

3. Siparuna diandra Duke, Ann. Missouri Bot. Gard. 49:546(234). 1962. TYPE: Panama, Terry and Terry 1496 (MO, holotype; F, isotype).

Shrub 2-3 m tall; dioecious; stems and branches terete; pubescence pilose, hairs up to 0.3 mm long, light brown to gray. Leaves opposite, obovate to subelliptic, membranaceous, 8-11 cm long, 3-4 cm wide; entire to slightly denticulate with the apical termination on the monimiod tooth cassidate; apex caudate acuminate; base attenuate-cuneate; 6-8 arched lateral veins; moderately stellate pilose above and below; petioles 0.8-1.5 cm long. Staminate inflorescence few flowered cymes; pedicels to 3 mm long; peduncles 0.8-1.2 mm long; pubescence gray stellate pilsoe to 0.3 mm long. Flowers white to green; stellate hairs on exterior, inside glabrous; receptacle wheel-shaped, obconic; up to 1.5 mm in diameter; velum dome shaped; tepals frequently 4, erect, becoming black when dry, 0.5 mm long; apical pore minute; stamens 2, keeled, hooded, fleshy to 1.5 mm long, scarcely exserted; pistillate inflorescence not seen. Aggregate fruit globose, 1-1.5 cm in diameter, red drying black, bursting irregularly exposing a light interior. Seeds 5 mm long, arillate structure covering the ovary with two lateral lobes.

Duke (1962) believed that this species has no close allies in Central America, but stated that it is closely related to the Peruvian *S. gilgiana*. *S. gilgiana* differs in having larger leaves and petioles and the tepals are connate into a repand flange.

DARIEN: Cerro Tacarcuna S slope 1250-1450 m, ridge top well below summit, Gentry & Mori 13936 (SCZ). Cana-Cuasi Trail, camp 2, 2000 ft, Terry & Terry 1496 (F, GH, MO).

4. *Siparuna domatiata* A. Gentry, Selbyana 2:40, pl. 12 C. 1977. TYPE: Panama, Liesner 1198 (MO, holotype; C, CAS, F, NY isotypes).

Small trees 1.5-4 m tall; dioecious; aromatic; seldom branching from base; stems and branches terete; pubescence stellate 0.2-0.4 mm long. Leaves opposite, elliptic to narrow obovate, rarely slightly asymmetrical, membranaceous, very fragile when dry; 10-40 cm long; 6-16 cm wide; subentire; apex nearly cuspidate to narrowly acuminate; base more or less auriculate with the saccate auricles forming hollow domatia; 9-13 pairs of lateral veins; pubescence stellate 0.2-0.4 mm long, sparse appressed stellate below and nearly completely glabrescent above; petioles 1-6 cm long, opposing nearly always of differing lengths, longer 1 to 2 times the length of the shorter. Pistillate inflorescence 3-7 flowers in axillary cymes; pedicels 0.3-0.5 mm long; peduncles 0.5-0.9 mm long. Flowers green maturing to yellow and orange; exterior of floral receptacle with appressed stellate hairs; receptacle obconic; 4 mm in diameter; velum slightly conical; tepals 4-5 minute nearly obsolete; apical pore 0.4 mm in diameter; styles 6-8, clearly exserted, bases surrounded with a short cylindrical neck, thus appearing connate at their bases. Staminate inflorescences of 4 to 10 flowers in axillary cymes; similar in size and shape to pistillate although more numerous; apical pore 1 mm in diameter becoming larger as stamens emerge; stamens 6 usually 4 outer and 2 inner, 1 mm long, filaments dilated, anthers valvate, minute, introrse, usually slightly exserted. Aggregate fruit ecallose, globose, 1.5 cm in diameter, capped by persistent annulus, pink-green to red, pedicels up to 1.5 cm long, bursting irregularly exposing a pink interior with 5-10 seeds. Seeds 5 mm long, gray with black splotches, tuberculate, arillate structures cover upper half of ovary, bright red.

Found in only three provinces on Panama, this species is not common. It occurs from 200-800 m and flowers from March to July usually fruiting from

September to November. No other species of Siparuna has domatia and S. domatiata is easily identified because of that character. In the field pistillate plants are difficult to locate and appear to be rare. Based on the flower, S. domatiata is closely related to S. vinosa, although the leaves of vinosa are much smaller.

COCLE: El Cope on Pacific slope, near sawmill, 2400 ft, Antonio 2165 (F, MO, MU, PMA). Vicinity of El Cope, on steep slope above stream, Antonio 5303 (MO, US). El Cope, near Rio Blanco, 600 ft, Antonio 5370 (F, MO, NY). Above El Potroso sawmill at continental divide N of El Cope, Sytsma & Andersson 4550 (MO). COLON: Along Rio Escandaloso near Mina Numero 2, 250 m, Antonio 1314 (MO). PANAMA: Llano-Carti Rd. 1 mi past sawmill on dirt road, 1200 ft, Antonio 3914 (F, MO). Llano-Carti Rd. 25 km from Panamerican Hwy., Antonio 5289 (MO). Along El Llano Carti-Tupile road, 12 mi above Pan-Am Hwy, 200-500 m, Liesner 1198 (CAS, MO, NY). 12 km N of Pan-Am Hwy. at El Llano, 400 m, Nee & Dressler 9376 (DUKE, PMA).

5. Siparuna dressleriana T. Antonio, sp. nov. TYPE: PANAMA, Province of Panama, Vicinity of Cerro Jefe, near Altos de Pacora, 2400 ft, Antonio 3250 (MO, holotype; F, PMA, NY, isotypes). Fig. 17, 18, 19, 20.

Arbor dioecus 3-9 m altus; ramulis teretibus, pilis stellato; folia opposita, ovata vel elliptica, 19-48 cm longa, 9-20 cm lata; dentata irregularity; apice acuta vel acuminata; base cordata vel auriculata; petiolo ad 8 cm longo. Inflorescentiae feminea in axillis foliorum; flores albis vel viridis vel subrosi, ad 2 cm in diametro tepalis 5-6, stylus 10-14. Inflorescentiae masculae in axillis foliorum, receptaculo obconico, 5-7 mm in diametro; staminibus 5.

Trees 3-9 m tall; dioecious; aromatic; seldom branching from base, stems and branches terete; pubescence sparse to densely pubescent with erect stellate hairs. Leaves opposite, ovate to obovate to elliptic, membranaceous, 19-48 cm long, 9-20 cm wide; margin irregularly dentate; apex acute to acuminate; base cordate to nearly auriculate with distinct teeth, unequal, older leaves more auriculate; 10-14 pairs of lateral veins; upper leaf surface glabrous or with appressed simple or stellate hairs, lower surface with moderate to dense, stiff erect stellate hairs to 0.8 mm long (evident without magnification), surface rough to touch; petioles up to 8 cm long, canaliculate, opposing nearly always of differing lengths. Pistillate inflorescence of 5 to 20 flowered axillary cymes, up to 4 cm long; peduncles to 3 cm long; pubescence stellate over much of the inflorescence. Flowers white to pale cream to green to pinkish; up to 2 cm in diameter; tepals 5-6, erect, green, particularly unequal when young, reflexed and their margins curled when older, venation on tepals clearly evident at flower ages; apical pore 1 mm in diameter; styles 10-14, exserted. Staminate inflorescence flowers more numerous than pistillate, up to 8 cm long; peduncles nearly erect and radiating from leaf axis, green and long; pedicels shorter; pubescence stellate throughout. Flowers white to pink; receptacle obconic; 5-7 mm in diamter; velum planar, glabrous; tepals, 5, small, triangular, 3-4 mm long; stamens 5, 5 mm long, 2 mm wide broadest at base, clearly exseted through apical pore 1.5 mm in diameter; anthers minute, introrse, 2 keeled, valvate. Aggregate fruit, ecallose, globose to reniform, to 3 cm in diameter, pink to red with persistent green tepals, densely pubescent, stellate hairs appear raised on wart like projections, bursting irregularly exposing a pink to white interior and numerous tuberculate seeds. Seeds 5 mm long, arillate structure covers the ovary with two lateral lobes.

This species is named in honor of Robert L. Dressler, who first pointed out the tree to me. His encouragement to new students of the Panamian flora is greatly appreciated. At present, S. dressleriana is known only from Panama. Morphologically it appears to be closely related to S. pittieri from Venezuela, but the leaves are much larger, and the floral structure is quite different. Steyermark described S. pittieri as having 4 united styles, but examination of the type specimen reveals that these are 4 united stamens not styles. The leaves of S. dressleriana are similar to S. quadrangularis from Ecuador but differs in not having quadrangular branchlets and much larger and more triangular tepals. The flowers of S. quadrangularis come close to those of S. spectabilis but the leaves differ in size, shape, and pubescence from those of S. dressleriana. The base of the leaf has a very distinct cordate shape (Fig. 19). Although the size of the flowers (Fig. 18) appear to vary greatly within this species, the distinctive leaf base make it easily recognizable. Flowering from November to February, the species can be found in fruit from February to April. The color of the flower varies from nearly white at Cerro Jefe in Panama Province to pinkish-green at Cerro Tute in the province of Veraguas.

COCLE: Cloud forest, El Valle 800-100 m, Duke 13144 (GH). Cerro Caracoral 2700-3200 ft, Dwyer & Correa (F, SCZ). Cerro Pilon, El Valle site area of WEPCOR, Kirkbride 1075 (F). PANAMA: Cerro Jefe area, near Altos de Pacora, 800-900 m, Antonio 4475 (F, PMA, MO). Vicinity of Cerro Jefe, Antonio 5312, 5313 (F, MO, NY). Cerro Jefe, 5.3 mi from Goofy Lake to top of Cerro, 900 m, Antonio 5387, 5388, 5389, 5389A (F, MO, NY, PMA). Cerro Campana, 2300 ft, Blum & Miller 2287 (SCZ). Cerro Jefe area, near Altos de Pacora, 600-950 m, D'Arcy & Sytsma 14736 (F, MO, NY, PMA). Cerro Jefe to La Eneida, Dwyer & Dressler 8201 (F, PMA). Cerro Jefe 6 mi past Cerro Azul on road to Altos de Pacora, 2600 ft, Sytsma & D'Arcy 3694 (F, MO, PMA). VERAGUAS: Vicinity of Escuela Agriculture Alto Piedra .3 mi beyond fork in road, near school toward Altlantic slope, 2800-3200 ft, Antonio 3466, 3491 (F, MO, PMA). Santa Fe, vicinity of Escuela Agricultura Alto Piedra, 2800 ft, Antonio 4000, 4032 (F, MO, PMA). Vicinity of Cerro Tute, 2900 ft, Antonio 5396, 5397, 5398, 5399, 5400, 5403 (F, MO, PMA). Cerro Tute, east slopes 1 km beyond Escuela above Santa Fe, 900-1200 m, Sytsma & Andersson 4652, 4704 (MO). Road past Escuela Agricola Alto Piedra above Santa Fe to continental divide, 900-1100 m, Sytsma & Andersson 4787 (F, MO).

6. Siparuna fimbriata T. Antonio, sp. nov. TYPE: PANAMA, Province of Veraguas, vicinity of Escuela Agricultura Alto Piedras, near Santa Fe along trail to top of Cerro Tute, 1200 m, Antonio 4928 (MO, holotype; PMA, F, isotypes). Fig. 21, 22, 23, 24, 25.

Arbor dioecus 3-4 m altus; ramulis teretibus, pilis stellato; folia opposita, ovata vel elliptica, 13-29 cm longa, 7-15 cm lata; dentata vel fimbriata; apice obtusa vel acuta; basi cuneata vel acuta; petiolo ad 7 cm longo; inflorescentiae feminea pauciflorigerae in axillis foliorum. Flores receptaculo conico 1 cm in diametro tepalis 5-6; stylus 10-15; inflorescentiae masculae pauciflorigerae in axillis foliorum. Flores albis vel viridis, receptaculo obconico 4-5 mm in diametro tepalis 5-6 fimbriatis; staminibus 4-5.

Trees 3-4 m tall; dioecious; aromatic; seldom branching from base, stems and branchlets terete, moderately to densely yellowish stellate pubescence. Leaves opposite, ovate to obovate to elliptic, membranaceous, 13-29 cm long, 7-15 cm wide; margins dentate to fringed, exaggerated serrations at the base of the leaf appear as fringed appendages, appendages themselves pubescent with stellate hairs, margin of leaf densely pubescent; apex obtuse to acute; base cuneate to acute; 10-15 pairs of lateral veins; upper leaf surface sparse to moderately pubescent, simple to stellate hairs to 1 mm long, lower leaf surface soft to touch; petioles up to 7 cm long, densely pubescent. Pistillate inflorescence of few flowered axillary cymes, 1-1.5 cm long, peduncles up to 8 mm long; pubescence stellate. Flowers white to green; pubescence on interior and exterior; receptacle conical; 1 cm in diameter; velum glabrous; tepals 5-6, a depression near the apex of each tepal present; styles 10-15, clearly exserted. Staminate inflorescence few flowered, 4-6 flowers, axillary cymes, 1-2 cm long; peduncles up to 2 cm long. Flower receptacle obconic; 4-5 mm in diameter; stellate pubescence present; tepals 4-6, fringed, ca. 3 mm long; stamens 4-5, 2 mm long, 1.5 mm wide, introrse, clearly exserted; anthers minue, valvate. Aggregate fruit escallose, globose to reniform, up to 2 cm in diamter, red to pink; tepal remnants reflexed toward base of fruit, slight stellate pubescence, bursting irregularly exposing a pink interior and tuberculate seeds. Seeds 5 mm long, arillate structure covers the ovary with two lateral lobes.

At present this species is known only from Panama, and is named for the fringe-like appearance of the base of the leaf (Fig. 22, 23). It flowers from December to June and has been collected in fruit during December and January. The margin of the leaf is very similar to that of Siparuna pectinata, but it otherwise differs greatly from that species.

COCLE: Vicinity of El Cope, near sawmill, Antonio 5306 (F, MO, PMA). Above El Potroso sawmill at continental divide N of El Cope, Sytsma & Andersson 4580 (MO). COMARCA DE SAN BLAS: Vicinity of the summit of Cerro Obu, 2400 ft, Antonio 5376 (F, MO, PMA). VERAGUAS: Vicinity of Cerro Tute, Antonio 5394, 5395 (F, MO, PMA). Past Santa Fe on Atlantic slope in forest along stream, 1200 ft, Hammel 8582 (F). Headwaters of Rio Caloveborita, 15 km past Escuela Agricola Alto Piedra above Santa Fe, 500 m, Sytsma & Andersson 4737, 4764 (F, MO, PMA).

7. Siparuna guianensis Aubl. Hist. Pl. Guian. Fr. 2: 865. 1775. TYPE: French Guiana, Sagot 857 (P, holotype not seen; GH type fragment).

Citrosma discolor Poepp. & Endl. Nov. Gen. & Sp. 2:48. 1817.

Citriosma guianensis (Aubl.) Tul. Monogr. 361. 1855.

Cistriosma guianensis B nuda Tul. loc. cit. 362. 1855.

Citrosma guianensis V divergentifolia Tul. loc. cit. 1855.

Siparuna panamensis A.DC. in Journ. Bot. 3:219. 1865.

Siparuna discolor A.DC. in DC. Prodr. 16: 656. 1868.

Siparuna guianensis B glabrescens A.DC. loc. cit. 654. 1868.

Siparuna guianensis V longifolia A.DC. loc. cit. 1868.

Siparuna guianensis 8 divergentifolia A.DC. loc. cit. 1868.

Siparuna foetida Barb. Rodr. in Vellosia 2^1:68. 1891.

Siparuna guianensis var. nitens O. Ktze. Rev. Gen. 3^2:276. 1898.

Citriosma glabrescens Mart. ex Tul., Monogr. 361. 1855.

Citriosma oblongifolium Spreng. ex Tul., Monogr. 361. 1855.

Angelina divergentifolia Pohl ex Tul., Monogr. 370. 1855.

Citriosma oligocarpa Mart. ex Tul., Monogr. 370. 1855.

Siparuna sprucei Rusby, in Mem. Torrey Bot. Club. 6:112. 1896.

Citriosma oblongifolia Leandr. ex Tul. in Monogr. 362. 1855.

Small trees or shrubs to 5 m tall; monoecious; aromatic; seldom branching from base; ultimate branches terete or slightly flattened; minute stellate hairs along branches 0.2 mm long, reddish-tomentose to glabrescent. Leaves opposite, elliptic to ovate, 9-19 cm long, 3.5-9 cm wide; entire; apex acute to long acuminate; base cuneate to truncate; 7-11 lateral veins on each side; mostly appressed stellate and simple to glabrescent above, stellate to simple to glabrescent below; petioles short 5-9 mm long, opposing not markedly different in length; leaf drying yellowish brown. Staminate inflorescence of 2-4 or 3-20 flowered cymes in each axil, sometimes helicoid-like; peduncles 3-4 mm long; pubescence pale yellow stellate throughout. Flowers green; floral receptacle 3 mm in diameter; velum lacking; tepals 4-6, deltoid to somewhat hemispherical seldom expanded; stamens 10-15, long exserted, unequal, 1-3 mm in length, filaments dilated; anthers minute, valvate flaps often extending 90° or more from the anther when open, no apical pore, stamens emerge through the deltoid tepals. Pistillate inflorescence similar to the staminate, flowers with 9-15 styles, long, usually connate into an exserted column; rudiments of velum sometimes present, obscured by tepals. Aggregate fruit ecallose, ovate, 1.3 cm in diameter when mature, 4-5 minute remnants of the tepals at base, green becoming shaded with red, stellate hairs unevenly distributed on exterior, bursting irregularly exposing the yellowish interior and 5-10 tuberculate seeds. Seeds 5 mm long, dark with white arillate structure completely covering the surface.

Siparuna guianenesis flowers from March through July and can be found in fruit from July to December. This species is widespread from Peru and Brazil to Columbia and Costa Rica. Standley (1928) reported that in Panama, the plant is supposedly a remedy for colic and a vermifuge on fowl. This species differs markedly from most other species of Siparuna in that it is monoecious, has a white arillate structure completely surrounding the seeds, and aromatically is unlike other species. Many species of Siparuna in Panama have lemon-like odors; guianensis foliage has a very disagreeable odor, reminiscent of wet chicken feathers.

CANAL ZONE: Vicinity of Gamboa, 3.8 mi from entrance to Pipeline Rd. Antonio 5293 (F, MO, MU, PMA, US). Barro Colorado Island, Aviles 16 (F). Shores of Lake Gatun, S of lab, BCI, Bangham 457 (F, GH). 3 mi NW of Gamboa Navy Pipeline Reserve Area, Correa 195 (PMA, SCZ). Along power line road near Madden Wye, Croat 14594, 15267 (F, NY, SCZ). Vicinity of Chagres, Fendler 188 (K). Pipeline Road, Gamboa, Foster 464 (DUKE). Woods near Gatun station, Panama Railroad, Hayes 149 (NY). Vicinity of Gatun, Hayes 364 (NY). In open woods near Panama, Hayes 671 (K). NW part of Canal Zone, W of Limon Bay, Gatun Locks and Gatun Lake, Johnston 1808 (GH). Near Fort Randolph, Maxon 6525 (US). 4 km NW of Gamboa, Pipeline Rd. 50 m, Nee 7071 (US). Barro

Colorado Island E shore, Salvoza 900 (GH). Barro Colorado Island, Gross Point, Shattuck 793 (F). 4-6 mi N of Gamboa along Pipeline Rd., Tyson 1489 (PMA, US). CHIRIQUI: Vicinity of San Felix, 100 m, Allen 3654 (F, GH, NY, US). In village of Las Lajas, Tyson 5612 (SCZ). COLON: Loma de la Gloria, near Fato, 10-104 m, Pittier 4077 (F, GH, K, NY, US). Vicinity of Pinas, Chagres 30 m, Lao & Holdridge 180 (DUKE, PMA). COMARCA DE SAN BLAS: Vicinity of Mulatuppu, Rio Ubedi, Duke 8464 (US). DARIEN: Vicinity of La Palma, 0-50 m, Pittier 6699 (US). HERRERA: Near Las Minas in La Cabuya, Carrasquilla 229 (F, PMA). Vicinity of Ocu, Ebinger 1091 (US). 12.5 mi S of Ocu, 1200 ft, Lewis 1634 (DUKE, K). PANAMA: Vicinity of Rio Taoia, Standley 28093, 28296 (US). VERAGUAS: 5 mi N Santiago vicinity of Santa Maria River, Blum & Tyson 608 (SCZ). Santiago, 2 mi from Transisthmian Highway towards Atalaya, Dwyer 7403 (DUKE).

8. Siparuna nicaraguensis Hemsl. Biol. Centr. Am. Bot. 3:69. 1882. TYPE: Nicaragua, Tate 385, 386, 421 (K, holotype not seen).

Shrubs or trees 2-8 m tall; dioecious; aromatic; occasionally branching from the base; ultimate branches terete; pubescence ferruginous stellate, the hairs evanescent 0.2 mm long. Leaves opposite, elliptic to obovate, membranaceous, 8-17 cm long, 4-8.5 cm wide; entire to undulate or minutely denticulate; apex more or less acuminate; base cuneate to rounded; 7-11 lateral veins on either side; glabrous to sparsely pubescent above, scantily stellate-pubescent to subglabrous below; petioles 1.5-6 cm long, unequal, that of one pair of leaves often twice as long as the other. Pistillate inflorescence slightly pendant, of 5-30 flowers in axillary cymes; peduncles mostly 2-5 mm long; flowers green becoming yellow to orange when mature; stellate puberulent except for inner portion of tepals and velum; well developed floral cup; 5-6 mm in diameter; tepals generally 4 sometimes 5, upright, 1-2 mm in length; styles 10-15, filiform, 1-2 mm in length exserted through apical pore. Staminate inflorescence similar to pistillate, flowers similar in size and shape, although more numerous; tepals triangular, wider at apex; apical pore 1.2 mm in diamter; stamens 6, 4 outer and 2 inner, exserted, filaments dilated, nearly 1 mm wide at base; anthers valvate, minute, introrse. Aggregate fruit ecallose globose, 1-2 cm in diameter, capped by the persistant erect tepals, orange to red speckled white, pubescence stellate, bursting irregularly exposing a pink to red interior and 5-23 tuberculate seeds. Seeds 5 mm long, gray with black splotches, arillate structure covers the ovary with 2 lateral lobes and is bright red.

Siparuna nicaraguensis is distinct among the Panamanian species because of its large erect green tepals. The species generally flowers from November through June and can be found in fruit from June through November. In Panama it is found at higher elevations usually around 600 m. It occurs from Panama to Mexico.

BOCAS DEL TORO: Regon of Almirante, Buena Vista Camp on Chiriqui Trail 3000 ft, Cooper 616 (F, K, NY, US). Between Buena Vista coffee finca and Cerro Pilon, Kirkbride & Duke 681 (NY, SCZ). COCLE: N rim of El Valle de Anton, Alson 1841 (F, NY, US). La Mesa cloud forest, El Valle de Anton 800 m, Kennedy 2085 (US). N rim of El Valle de Anton, near Cerro Turega 650-700 m, Woodson & Schery 159 (US). PANAMA: Vicinity of Cerro Campana, Antonio 5296, 5390, 5309, 5405 (MO). Cerro Campana, 2300 ft, Blum 2368 (GH, SCZ).

Wet forest Cerro Campana 850 m, Busey 873 (F, GH, NY, PMA, US). Vicinity of Cerro Campana 2300 ft, Correa & Dressler 872 (DUKE, PMA). Moist slopes of Cerro Campana, Croat 12111 (GH). Cerro Campana 3000 ft, Duke 10736 (DUKE). Summit of Cerro Campana, Dwyer 4832 (F, NY). La Campana, Campana, Ebinger 333, 336 (US). NE side of Cerro Trinidad, 850 m, Foster 2095 (DUKE, F, PMA). Path ascending to Cerro Campana, Garner 6 (DUKE, PMA, SCZ). Cerro Campana 800-1000 m, Gentry 1824 (US), 4921 (F, NY). Cerro Campana cloudforest 800 m, Kennedy 488 (DUKE, US). On trail to mountain with cross Cerro Campana, Kirkbride 253 (C, NY). Between peaks of Cerro Trinidad, saddle on SE slope, Kirkbride & Duke 1644 (NY). Upper slopes of Cerro Campana 207 m, LeDoux 2572 (CAS). Cerro Campana 850 m, Liesner 626 (C, AS, F, NY). 8.6 mi SW of Capira, Cerro Campana 700 m, Luteyn 956 (F, DUKE). Cerro Campana cloud forest 850 m, Luteyn 3987 (DUKE). Cerro Campana cloud forest, Luteyn & Kennedy 1806 (DUKE, F, GH). Near Cerro Campana, 3080 ft, Mendez 73, 75 (PMA). Summit of Cerro Campana, Porter 4187 (DUKE, NY), 4214 (F, NY), 4969 (DUKE, F). Cloud forest and road banks in vicinity of Cerro Campana 2500-2900 ft, Utley 5709 (DUKE). Dry slopes of Cerro Campana, 2500-2900 ft, Wilbur 24362 (DUKE). Cerro Campana, 2700 ft, Wilbur & Weaver 11287 (CAS, DUKE, GH, NY, PMA, US).

9. Siparuna patelliformia Perk., Engl. Bot. Jahrb. 28:692. 1901. TYPE: Costa Rica, Oersted 2, 3 (C, holotype; GH, type fragment).

Shrubs or small trees 1.5-4 m tall; dioecious; aromatic; multistemmed from base; branches subterete; densely tomentose yellow, older stems less tomentose. Leaves opposite, variable shape, obovate to ovate to obovate-oblong to rarely lanceolate, coriaceous, up to 1 mm thick, 9-22 cm long, 3.5-7 cm wide; entire to shortly undulate to denticulate; apex obtuse to acute to rarely short attenuate; base obtuse to cordate to rarely lobate; 10-14 lateral veins, upper embedded, lower prominent conspicuously more tomentose; densely tomentose on both upper and lower surface, dark green above, pale green below, drying yellowish-green somtimes organgish, velvety texture; petioles 1.5-3 cm long, up to 4 mm wide, opposing sometimes of differing lengths, tomentose yellow. Pistillate inflorescence of few flowered short axillary cymes, sometimes cauliflorous, usually 2-3 flowers pendant on either side of the petiole; pediels 3-4 mm long; flowers yellowish-green to yellow; entire receptacle and velum densely tomentose; receptacle dish-shaped; 4-5 mm in diameter; velum undulate; tepals obsolete; apical pore 1 mm in diameter; styles 7-12 clearly exserted through aperture-like pore, styles united at middle. Staminate inflorescence similar in pubescence and shape to pistillate; stamens 6 sometimes 8, usually 4 outer and 2 inner, filaments dilated, 2 mm long, 1 mm wide; anthers minute, valvate, introrse, usually exserted. Aggregate fruit ecallose, globose, 1-1.7 cm in diameter, capped by a minute perisitent annulus, dull red with tomentum, velvety surface, bursting irregularly exposing a red interior and few tuberculate seeds. Seeds 5 mm long, gray with black splotches, arillate structure covers the ovary with two lateral lobes and is bright red.

This species has a citronella-like odor and occurs at high elevations 500-1200 m. It flowers from October to February and has been collected in fruit from

October to June. This treatment extends the range of S. patelliformis into Panama from Costa Rica. S. patelliformis was long considered to be endemic to Costa Rica but the Panamanian material is clearly patelliformis. S. patelliformis has leaves which are very similar to S. sauraurifolia, but the inflorescence of S. sauraurifolia is much longer. Field observations indicate that this is probably the only species of Siparuna that leaf cutter ants attack in Panama.

PANAMA: Cerro Jefe, 5.3 mi from Goofy Lake to top of Cerro, 900 m, Antonio 5310, 5311, 5368, 5369, 5378, 5379, 5380, 5381, 5382, 5383, 5384, 5385, 5386 (all F, MO). 7 mi N of Cerro Azul on rd. to Cerro Jefe, 2600 ft, Blum, Tyson & Godfrey 1803 (SCZ). Cerro Jefe area, near Altos de Pacora, 600-950 m, D'Arcy & Sytsma 14724 (MO). Cerro Jefe to 3100 ft, Dwyer & Gentry 9428 (F). E slope of Cerro Jefe, 2700-3000 ft, Gentry 3336 (SCZ, GH). Cerro Azul, 1-2 mi beyond Goofy Lake, Gentry, Dwyer & Tyson 3420 (DUKE). Cerro Jefe 1000 m, Gentry 6764 (GH, PMA). Cerro Jefe-La Eneida, Kennedy 1168 (DUKE). 2-3 mi S of Goofy Lake, road to Cerro Jefe, 2000-2200 ft, Lewis 258 (F, GH). Altos del Rio Pacora, 2500 ft, Lewis 2332 (F). Vicinity of Cerro Jefe, 3000 ft, Systma 1417 (MO). Cerro Jefe, 4 mi past Cero Azul on road to Altos de Pacora, 2800 ft, Systma 3982 (MO). Cerro Jefe cloud forest, 4-5 mi past Cerro Azul, 900-1000 m, Sytsma 4111 (MO). Cerro Jefe cloud forest, 4-5 mi past Cerro Azul, 900-1000 m, Systma 4115 (MO). Cerro Jefe forest at 2700-3000 ft, Tyson, Dwyer & Blum 3295 (SCZ). Along road past Cerro Azul, 2600 ft, Tyson & Lazor 6204 (PMA).

10. Siparuna pauciflora (Beurl.) A.DC. in DC Prodr. 16^2:656. 1868. TYPE: Panama, Billberg 325 (B, holotype destroyed, fragment seen, GH).

Citriosma pauciflora Beurl. Vet. Akad. Handl. Stockh. 1854:144. 1856. Siparuna cauliflora Hemsl. Biol. Centr. Am. Bot. 3:69. 1882. ISOTYPE: Panama, Fendler 196 (US).

Trees 2-7 m tall; dioecious; aromatic; may branch from the base; stems and branches terete to quadrangular; hairs 0.3-0.5 mm long. Leaves opposite, broadly elliptic to obovate, 10-40 cm long, 7-16 cm wide; rarely entire to serrate, often with the apical termination on the monimiod tooth is cassidate and sometimes with a spherulate apex; apex acute to acuminate; base cuneate to decurrent; 10-20 pairs of lateral veins; pubescence rarely absent, often of branched hairs, simple also present, when present more abundant on lower surface than upper; petioles 1.5-4.5 cm long, canaliculate, nearly always of differing lengths, longer up to 1.5 times the length of shorter. Pistillate inflorescence of 5-15 flowered sessile axillary cymes, often cauliflorous, pedicels 2-10 mm long; flowers green maturing to yellow and orange; gray to yellow stellate pubescence over much of the receptacle and velum; well developed floral cup, slightly firm but fleshy, obconical; 6-10 mm in diameter; 5 mm in length; velum planar; tepals connate forming a dish-shape; apical pore 1.2-2.5 mm in diameter; styles 10-30, separate, filiform, 3 mm in length. Staminate inflorescence of 5-25 flowers, subsessile axillary cymes, similar in pubescence and shape but smaller than pistillate flowers; peduncles 1-5 mm long; pedicels 2-10 mm long; apical pore 1-1.5 mm in diameter; stamens 10-30, 2 mm in length; filaments dilated, 0.7-1 mm wide; anthers minute, valvate, introrse, usually slightly exserted. Aggregate fruit ecallose, globose, 1-2.5 cm in diameter, capped by the persistant annulus, greenish-yellow, drying black, pubescence stellate, bursting irregularly exposing a white interior and 5-32 tuberculate seeds. Seeds 5 mm long, gray with black splotches, arillate structure covers the ovary with two lateral lobes and is bright red.

Siparuna pauciflora is the most common species of Siparuna in Panama, and is found in nearly every province of Panama from sea-level to 900 m. It ranges from Costa Rica to Peru and is characterized by its disk-shaped flowers and rather large globose green fruit. In Costa Rica its common name is limoncillo. This species flowers beginning in the dry season from early December until early May, the pistillate plants commence flowering approximately a month before the staminate individuals (Antonio, 1983). It is the only species of Siparuna in Panama with pale green fruit and green disk flowers.

BOCAS DEL TORO: In old cemetry 1.5 mi W of Almirante, Blum 1355 (SCZ). Region of Almirante, Daytonia Farm, G. P. Cooper 69 (F), 513 (F, K), 422 (US, F, K). Region of Almirante, Buena Vista Camp of Chiriqui Trail 1250 ft, Coope 589 (F). Changuinola Valley, Farm six, Dunlap 489 (US, F). Cloud forest above Quebrada Huron on Cerro Bonyik, 15-360 m, Kirkbride & Duke 589 (NY). Vicinity of Chiriqui Lagoon, Old Bank Island, Von Wedel 2165 (US, GH), 1968 (GH), 2085 (GH). CANAL ZONE: Mojinga Swamp, near mouth of Rio Chagres 1 m, Allen 908 (US). Vicinity of Pipeline road, Antonio 5404 (MO, F). Barro Colorado Island, Bailey 327 (F). Vicinity of Cerro Viejo on K 16C, Blum 1240 (SCZ). Vicinity of Ft. Sherman, Blum & Dwyer 2111 (GH, SCZ). Cruces Trail, Bartlett & Lasser 16454 (DUKE, GH). 4 km S of river on road to Bamboa and Summit, Busey 391 (F, GH). Roadside Madden Forest road 1, Croat 8940 (SCZ). Barro Colorado Island, Standley Trail 1100, Croat 8337 (SCZ). Barro Colorado Island, Shannon Trail 400, Croat 8232 (F, SCZ). Barro Colorado Island S M Trail 100, Croat 5839

(F, SCZ). Barro Colorado Island, Zetek Trail 900, Croat 6648 (F, SCZ). Barro Colorado Island, Wheeler Trail 1250, Croat 6284 (F, DUKE, SCZ), Croat 7321 (SCZ), Croat 1275 (F). Barro Colorado Island, Vantyne Trail 600, Croat 7818 (F, SCZ). Barro Colorado Island, Wheeler Trail 1210, Croat 13216 (F, DUKE). Albrook, U.S. Army Tropical Test Center Site, Dwyer & Robyns 122 (US). Barro Colorado Island, Donato Trail, Ebinger 62 (US). Vicinity of Chagres, Fendler 196 (GH). Barro Colorado Island, Armour Trail, Foster 866 (DUKE). W of Limon Bay, Gatun Locks and Gatun Lake, Johnston 1525 (GH). N of Gamboa, Pipeline Rd. 1 mi past marker 75, Kennedy 464 (CAS, PMA, DUKE). Barro Colorado Island, Kenoyer 469 (US). Pipeline Rd. N of Gamboa, Luteyn 1549 (DUKE, F, GH). Trail near reservoir 1-3 mi from Gorgona, Maxon 4742 (F, G, GH, US). Pipeline Rd. 15-20 mi NW of Gamboa 0-100 m, Mori & Kallunki 1720 (US). 1.5-2 km N of Gamboa, 35-50 m, Nee 9407 (US). 6 km E of Gamboa, Rd. C 29 N of Las Cruces Trail, 150 m, Nee 9045 (DUKE). Near Fort Lorenzo, mouth of Rio Chagres, Piper 5913 (US). Vicinity of Frijoles, Piper 5823 (US). Along Cano Quebrado, Pittier 6660 (GH, US). Near Las Cruces, 20-100 m, Armour Trail 3, Shattuck 1050 (F, US). Barro Colorado Island, Standley 31301, 31428, 40854 (US). Vicinity of Ft. Sherman, Standley 31043 (US). Barro Colorado Island, Zetek Trail, D. E. Starry 38 (F). Vicinity of San Lorenzo, Tyson & Blum 3678 (SCZ). On road to old cacao plantation near Summit Gardens, Tyson & Lazor (PMA). Barro Colorado Island, Donato Trail, Wetmore & Abbe 121 (GH). Barro Colorado Island, Zetek Trail, Wilbur & Weaver 10814 (DUKE). Barro Colorado Island, Nemesia Trail, Wilson 32 (F). Barro Colorado Island, Shore W of Pt. Salud, Woodworth & Vestal 421 (F, GH). Barro Colorado Island, J. Zetek 3695 (F). COCLE: N rim of El Valle de Anton, 600-1000 m, Allen 1636 (F, GH, US). 7 km from Llano Grande on road to

Coclesito near continental divide, 1200 ft, Antonio 1380 (F, MO). 4 mi N of Llano Grande on road to Coclesitio, 600 m, Antonio 3606 (F, MO). Vicinity of El Cope, near sawmill, Antonio 2132, 5297 (Both F, MO). Above La Pintada, peak E of Llano Grande-Toabre highway, 1400-1900 ft, D'Arcy & Sytsma 14701 (MO). 2 mi N of Cerro Pilon, 900 m, Liesner 714 (CAS, DUKE, G). 8 mi N of El Valle de Anton, Luteyn & Kennedy 1675 (DUKE, GH, F). NE slopes of Cerro Caracoral, N rim of El Valle, 2700-3200 ft, Sytsma 3758 (MO). 15-20 km NE of La Pintada towards Toabre, 600-1000 ft, Sytsma & D'Arcy 3628 (MO). COLON: Near Peluca 25.6 km from Transisthmian Highway on road to Nombre de Dios. Up stream on tributary to Rio Boqueron, Kennedy 2652 (F, US). Vicinity of Salud 50 m, Lao & Holdridge 208 (PMA). N side of Rio Guanche, ½ km upstream from Puerto Pilon-Portobello Rd. 5-20 m, Nee 7097 (DUKE, US). Brushy woods above road, 2.9 mi SW of Portobelo on road to Pilon, Nee & Mori 3666 (PMA). Near Portobelo, 5-100 m, Pittier 2430 (GH, US). Between France Field, Canal Zone and Catival, Standley 30300 (US). COMARCA DE SAN BLAS: Near mouth of Rio Masarganti on trial to top of Cerro Obu, 0-60 m, Antonio 5366 (F, MO, US). Vicinity of Aligandi River, Duke & Bristan 335 (US). DARIEN: N of Punta Guayabo Grande, 200-600 ft, Antonio 5349 (F, MO). 10 km NE of Jaque, slopes of RIo Tabuelitas above Biroqueira, Indian village on Rio Jaque below mouth of Rio Pavarando 10-150 m, D'Arcy & Systma 14465 (MO). 10 km NE of Jaque, headwaters of Rio Pavarando 1400 ft, D'Arcy & Systma 14507 (MO). S slopes of Cerro Tacarcuna above Rio Pucuro 700-1000 m, Gentry & Mori 13898 (PMA). Banks of Rio Paca, Stern 715 (GH, US). Vicinity of Camamento Buena Vista, Rio Chucunaque above confluence with Rio Tuquesa, Stern 829 (GH, US). 10 km NE of Jaque, slopes of Rio Tabuelitas, 400 ft, Systma & D'Arcy 3289, 3315 (F, MO). Cana-Cuasi Trail, camp 2, Chepigana District, Terry 1474 (F), 1455 (GH). Periaque camp at River, Tyson 4739 (SCZ). LOS SANTOS: Loma Prieta, Cerro Grande 2400-2800 ft, Lewis 2191 (F). Vicinity of Tonosi, Guanico, 117 ft, Stern 33668 (US). PANAMA: Cerro Campana, 2700 ft Antonio 5308, 5391, 5392 (F, MO). 5 mi N Cerro Azul, on road to Cerro Jefe, 2400 ft, Blum 1702 (PMA). Cerro Campana, along trail to top, Correa & Dressler 294 (DUKE). Near Rio Cascadas, Capetal de Lopez, 300-400 m, Correa & Dressler 1659 (PMA). 5 mi above Interamerican Hwy. on road to Cerro Azul, Croat 11499 (F, SCZ). Cerro Campana on edge of trail, Garner 18 (DUE, PMA, SCZ). Cerro Campana 1 mi past Florida State U. Field Station. 800 m, Kennedy 1535 (PMA, US), 484 (DUKE). 1 mi N of junction of the Cerro Azil road and the road to transmission tower, Lazor 5532 (SCZ). Cerro Campana, LeDoux 2610 (CAS). SE slopes of Cerro Campana, Lewis 3-66 (F). Cerro Campana, 850 m, Liesner 622 (CAS, DUKE, F, G, GH). Cerro Campana, near Motel Su Lin, 3100 ft, Mendez 165 (PMA). 3 km S of Alcalde Diza near Cerro Penon, Nee 8885 (GH). Cerro Campana above Su Lin Motel, Porter 4268 (F), 4213 (DUKE). Rio Tapia, Standley 28265 (GH), Vicinity of Rio Tecumen, Standley 26752 (F), 29348 (US). Juan Diaz, Standley 30588 (US). Cerro Azul, 2000 ft, Tyson 2195 (SCZ). 1 mi N Cerro Azul at 2300 ft, Tyson & Blum 4092 (SCZ). Dry slopes of Cerro Campana, 2500-2900 ft, Wilbur 24365 (DUKE). VERAGUAS: near Santa Fe along trail to top of Cerro Tute, 2800 ft, Antonio 3993 (F, MO). Vicinity of Escuela Agricultura Alto Piedra, near Santa Fe, 3600 ft Antonio 4990, 4942 (both F, MO). Vicinity of Cerro Tute, 2900 ft, Antonio 5402, 5410 (both F, MO). Alto Piedra near Sata Fe 1200 m, Lao 520 (PMA). 7 km W of Santa Fe on road past agricultural school, 2900 ft, Nee 11231 (US). Cerro Tute, E slopes 1 km beyond Escuela Agricola Alto Piedra above Santa Fe, 900-1200 m, Sytsma & Anderrson 4629 (MO, PMA).

11. Siparuna riparia (Tul.) A.DC., DC. Prodr. 16^2: 647. 1868. TYPE: Mexico, Galeotti 269 (GH, holotype; photo F).

Citriosma riparia Tul. Ann. Sci. Nat. 4^3: 36. 1855.

Siparuna riparia var. macrophylla Perk. Engl. Bot. Jahrb. 28: 690. 1901.

Siparuna riparia var. grandiflora Perk. Engl. Pflanzenr. 4. Fam. 101: 99. 1901.

Siparuna riparia var. calantha Perk. Notizbl. Bot. Gart. Berl. 10: 164. 1927.

Trees or shrubs 3-5 m tall; dioecious; slightly aromatic; the ultimate branches terete or quadrandular, tomentose with yellowish or reddish stellate hairs up to 0.2 mm long. Leaves opposite, elliptic to obovate often inequilateral, membranaceous, 7-14 cm long, 2.5-5 cm wide; serrate, often with the apical termination on the monimiod tooth is cassidate and sometimes with a spherulate apex; apex acute to caudate acuminate; base cuneate; 8-10 lateral veins on either side; pilose, especially below with stellate hairs up to 0.5 mm long; petioles 1-4.5 cm long, opposing nearly always of differing lengths, stellate hairs present. Pistillate inflorescence of 2-7 flowered axillary cymes, up to 2 cm long; peduncles 5-10 mm long; pedicels 3-9 mm long; gray to yellow stellate hairs over much of the inflorescence; flowers yellow to greenish-white; gray to yellow stellate pubescence over the receptacle except the velum; well developed floral cup; conical; 3-4 mm in diameter; 4-7, at first triangular, ultimately rounded and somewhat reflexed, apical pore 1-1.3 mm in diamter; styles 6-12, connate near the orifice, long exserted. Staminate inflorescence of 2-10 flowered cymes in each axil, similar to pistillate inflorescence only more flowers per axil; stamens

5-6, outer 4 disposed in a circle but not connate; anthers minute, introrse, clearly exserted, bivalvate flap over anther is nearly translucent. Aggregate fruit ecallose globose, 1-1.5 cm in diameter, pink to rose red, drying black, bursting irregularly exposing a white to pink interior and numerous tuberculate seeds. Seeds 5 mm long, arillate structure covers the ovary with 2 lateral lobes.

Siparuna riparia in Panama is known only from the province of Chiriqui. It is characterized by having minute flowers and small leaves with serrate margins. This species is known to flower from January to July and has been found in fruit in August. The species ranges from Mexico to Columbia. Although Perkins has said that the stamens number 10-12, Bourgeau 1748 identified as S. riparia by Perkins has 5-6 stamens, and Duke points out that this is probably the more prevalent number.

CHIRIQUI: Vicinity of La Fortuna, 9.3 mi from Plano de Hornito, Antonio 5264 (F, MO, NY). Cerro Forqueta 700 ft, Blum & Dwyer 2639 (SCZ). N.O. del campamento Fortuna (Hornito), sitio de presa, 1100 m, Correa & Dressler 2523 (DUKE, F, PMA). Vicinity of Bajo Chorro, Davidson 242 (F, GH). Cerro Horqueta 1666-2333 m, Kirkbride 144 (NY). Vicinity of Bajo Mona and Quebrada Chiquero, 1500 m, Woodson & Schery 600 (GH).

12. Siparuna rosicosta T. Antonio, sp. nov. TYPE: PANAMA, Province of Panama, Llano-Carti Rd., 25 km from PanAmerican Hwy., Antonio 5290 (MO, Holotype; F, PMA, isotypes). Fig. 26, 27, 28.

Frutex dioecia 1-3 m alta; ramulis teretibus, pilis stellato; folia opposita, angusta elliptica vel elliptica, 18-36 cm longa, 8-12 cm lata; integra vel undulata vel dentata; apice attenuata vel acuta; basi cuneata; petiolo 1-6 cm longo, basi rubello; inflorescentiae feminea paucifloriger in axillis foliorum. Flores receptaculo patelliformi 5-8 mm in diametro tepalis obsoletus; stylus 10-15; inflorescentiae masculae paucifloriger in axillis foliorum. Flores viridis vel luteus, receptaculo 4-5 mm in diameter; staminibus 4(6).

Shrubs or treelets 1-3 m tall; dioecious; aromatic; stems and branches terete, frequently reddish-brown, minute stellate hairs present. Leaves opposite, narrow elliptic to elliptic, frequently assymmetrical, 19-36 cm long, 8-12 cm wide; entire to undulate to rarely dentate; apex attenuate to acute; base cuneate; 12-14 pairs of lateral veins; upper surface glabous to sparsely pubescent, lower surface moderately to densely stellate pubescent; petioles 1-6 cm long, reddish at base, color extending into lower very prominent midvein, moderate to densely woolly pubescent stellate hairs; frequently dark green above and gray green below. Pistillate inflorescence few flowered cymes, up to 1 cm long, peduncles 3 mm long; flowers green to yellow, nearly sessile; glabrous to sparsely stellate pubescent; receptacle disk-shaped; 5-8 mm in diameter; velum glabrous; tepals obsolete or minute; apical pore 1-1.5 mm in diameter; styles 10-15, filiform, clearly exserted. Staminate inflorescence similar to pistillate but smaller in size and frequently more flowers present, peduncles longer than 3 mm, flowers green to yellow, glabrous to sparsely pubescent exterior; receptacle 4-5 mm in diameter; velum glabrous; apical pore 1 mm in diameter; stamens mostly 4 (6), sometimes connate at filament; anthers valvate, minute, introrse, usually slightly exserted. Aggregate fruit ecallose, globose, 1-1.5 cm in diameter, capped by yellowish-green persistent annulus, bright red, drying black, slightly pubescent, bursting irregularly exposing a pink interior and few tuberculate seeds. Seeds 5-6 mm long, gray with black splotches, arillate structure covers the ovary with 2 lateral lobes, bright red.

Siparuna rosicosta is characterized by its large narrowly elliptic leaves (Fig. 26) and is named for its prominent and frequently pale red lower midrib and red petiole. The flowers (Fig. 28) are similar to those of S. vinosa to which it is probably closely related. At present S. rosicosta is known only from Panama, flowering from August to March and fruiting from September to May.

COCLE: 4 mi past Llano Grande on road to Cascajal, ca. 2 mi W of continental divide, 600 m, Sytsma 3967 (MO, PMA). COLON: Trail from Rio Piedras to Santa Rita Ridge, 2200 ft, Antonio 3865 (F, MO, PMA). Trail from end of Santa Rita Ridge road to Rio Piedras, 600 m, Antonio 3735 (F, MO). District of Portobello, stream of N slope of Rio Gatun Drainage, 1600-1800 ft Antonio 3855 (F, MO, PMA). Santa Rita Ridge road, near end of trail 400 m, Antonio 4515 (F, MO, PMA). Vicinity of Rio Piedras along road to Puertobello, Blum 2513 (SCZ). Along Santa Rita Ridge lumber road, Correa & Dressler 989 (SCZ). Santa Rita Ridge, D'Arcy 6150 (C, PMA). Santa Rita lumber road 15 km E of Colon, Dressler & Lewis 3722 (PMA). Semi-swampy floodplain near bridge over Rio Buenaventura near Portobello, Foster 1795 (DUKE, PMA), 2064 (DUKE). Santa Rita Ridge, 4-5 mi from Transisthmian Hwy. Gentry 1886 (F, PMA). Santa Rita Ridge road 4 mi from Transisthmian Hwy. to Agua Clara, 500 m, Gentry 8857 (F). Santa Rita Ridge, 200-300 m, A. Gomez-Pompa 3135 (PMA). Portobello, semi-inundated forest near bridge over Rio Buenaventura, Kennedy 466 (DUKE, PMA). Portobellow Buenadventura, first bridge on road leaving from Portobello, Kenney

471 (PMA). Santa Rita Ridge, end of road from Transisthmian Hwy. ca. 10 mi from highway, Porter 4749 (GH). Ridge between Rio Piedras and Rio Gatun watersheds along trail from end of Santa Rita Ridge, 5-8 km SW of Cerro Bruja, Sytsma 4182, 4196, 4274 (MO). Upper Rio Piedras headwaters, along trail from end of Santa Rita Ridge Road, 11 km SW of Cerro Bruja, Systma 4261 (MO). Santa Rita Ridge, 7 mi from Transisthmian Hwy. 650 ft Wilbur, Almeda, Luteyn & Utley 15072 (F, CAS). COMARCA DE SAN BLAS: Near the mouth of Rio Masarganti on trail to top of Cerro Obu, 60 m, Antonio 5353, 5360, 5361, 5362, 5363, 5364, 5365, 5367 (F, MO, PMA). Vicinity of the Summit of Cerro Obu, 2400 ft, Antonio 5377 (F, MO). Trail to top of Cerro Obu, 500-1200 ft, Antonio 5374 (F, MO). PANAMA: Llano-Carti Rd. 1 mi past sawmill on dirt rd., Antonio 2523 (F, MO). Cerro Jefe, 3100 ft, Dwyer & Gentry 9411 (PMA). Km 10-12 on road to Carti, Kennedy & Dressler 3350 (US). Llano-Carti Rd. 6 mi from Pan-American Hwy. Sytsma 3999 (MO). El Llano-Carti Rd., 8 mi from Pan-American Hwy., Sytsma 4008 (MO).

13. Siparuna sytsmania T. Antonio, sp. nov. TYPE: PANAMA, Province of Bocas del Toro, NW ridge of Cerro Pate Macho from summit to Finca Serrano, 1200-2100 m, K. Sytsma 4899 (MO, holotype; F, PMA, NY, isotypes). Fig. 29.

Liane dioecus 2-3 cm diametro; caulis pilis stellato; folia opposita vel ternata, orbiculata, 8-13 cm longa, 5-9 cm lata; rare integra vel serrata; apice acuminata; basi rotundata; petiolo 2.5-2.5 cm longo; inflorescentiae feminea in axillis foliorum. Flores receptaculo patelliformi 5 mm in diametro tepalis 4-6; stylus 7. Flores masculei nunc ignoti.

Woody liana, 2-3 cm dbh; dioecious; stems sparse to moderately covered with yellowish stellate hairs. Leaves opposite, suborbiculate, 8-13 cm long, 5-9 cm wide; rarely entire to serrate, often with the apical termination on the monimiod tooth cassidate and sometimes with a spherulate apex; apex acuminate; base rounded; 7-9 prominent veins on lower surface; pubescence rarely absent, sparse to moderate yellowish stellate hairs on upper and lower surfaces; petioles 2.5-3.5 cm long, opposing sometimes of differing lengths, moderate to dense yellowish stellate hairs. Pistillate inflorescence of 5-15 flowered axillary cymes; peduncles to 1 cm long; pedicels 1-1.4 cm long; yellowish stellate hairs over much of the inflorescence; flowers green to orange; well developed cup; 5 mm in diameter; velum planar stellate hairs absent; tepals 4-6 rounded; apical pore 1 mm in diameter; styles 7 to many, 1 mm long, clearly exserted beyond surface of velum. Staminate inflorescence not seen. Aggregate fruit ecallose, globose, 1-1.5 cm in diameter, red, sparse minute stellate hairs ca. 0.2 mm long, stellate hairs along the persistent annulus, in clumps of 8-14; style remnants evident, bursting irregularly exposing a pink interior and 7-10 tuberculate seeds. Seeds 5 mm long, arillate structure covers the ovary with two lateral lobes.

At present, this species is known only from Panama, and is named after Kenneth Sytsma who first collected it. It is the only species of Siparuna in Panama with a vine-like habit. The suborbiculate leaf (Fig. 29), distinguishes it from all other species of Siparuna in Panama.

14. Siparuna tetraceroides Perk. Engl. Bot. Jahrb. 28:689. 1901. TYPE: Central America, Oersted (GH, type fragment).

Trees to 5 m tall; dioecious; aromatic; branches terete, hairs grayish-yellow to 0.3 mm long. Leaves opposite, elliptic to oblong, 11-18 cm long, 4.5-7 cm wide; undulate denticulate; apex short acuminate; base cuneate to cuneate rounded; 8-12 pairs of lateral veins; upper surface sparsely pubescent with simple and branched hairs rarely stellate, lower surface sparse to moderately pubescent with branched hairs, stellate hairs prominent on veins; petioles 1-3.5 cm long, yellow tomentose. Pistillate inflorescence few flowered axillary cymes, up to 1.5 cm long, pedicels to 1 cm long; flowers greenish yellow; exterior with simple to branched hairs; well developed floral cup, disk-shaped; to 6 mm in diameter; velum glabrous and slightly conical; tepals obscure to deltoid; apical pore 0.8 mm in diameter; styles to 15, barely exserted through the aperture like pore which is rimmed. Staminate inflorescence similar in shape and pubescence to pistillate but flowers are more numerous; pedicels to 1 cm long; flowers pale yellow to green; 4 mm in diameter; apical pore 1 mm in diameter; stamens 5-8, the 4 exterior in a whorl or often connate or connivent, 1.5-2 mm long; anthers minute, introrse, exserted. Aggregate fruit ecallose, globose to slighlty reniform, 1.5 cm in diameter, capped by minute remnants of the persistent tepals, pink to red, drying black, bursting irregularly exposing a white interior and several tuberculate seeds. Seeds 5 mm long, arillate structure covers the ovary with two lateral lobes.

In Panama this species occurs only in the province of Chiriqui. It was previously thought to be endemic to Costa Rica.

CHIRIQUI: Quebrada Tuco, 9 mi S of Puerto Armuelles 0-150 m, Croat 22106 (F). Between El Hato (Volcan) and Costa Rica, Ebinger 813 (F). Santa Clara region, 27 km NW of El Hato del Volcan on the upper and lower coffee finca of Ratabor Hartman, LeDoux 2654 (CAS, MO, NY). Quebrada Quanabentio beyond La Repressa 2 mi SW of Puerto Armuelles 0-200 m, Liesner 128 (F, NY). Forest around Puerto Remedios, 0-30 m, Pittier 3386 (F, US).

15. Siparuna tonduziana Perk., Engl. Bot. Jahrb. 31: 746. 1902. TYPE: Costa Rica, Tonduz 12766 (MA, holotype; US, isotype, GH, type fragment).

Trees 3-6 m tall; dioecious; aromatic; multi-stemmed, stems and branchlets terete, reddish-brown pubescence dense; stems frequently hollow. Leaves opposite, obovate to oblong, mostly inequilateral, 16-44 cm long, 9-27 cm wide; coarsely and irregularly dentate, hairs extending over margin by as much as 1-3 mm; apex acute to obtuse; base rounded or cordate; 14-17 lateral veins; lower surface moderately to densely pubescent, simple to stellate hairs, up to 2.5 mm long; upper surface moderately to densely pubescent, predominantly simple hairs up to 2 mm long; midvein densely yellow pubescent; midvein and lateral vein on lower surface dark red; petioles p to 6.5 cm long, canaliculate, drying reddish-brown, densely wolly pubescent. Pistillate inflorescence few flowered 4-7, axillary cymes up to 1 cm long, erect; pedicels 5 mm long; flowers receptacle conical, asymmetrical, hairs dense on receptacle exterior, 1 cm in diameter; velum glabrous, pink to white; tepals 5-6, white to greenish-red, triangular, hairs extending over margin, depressions in tepal apex; apical pore 0.5 mm in diameter;

styles 7-10. Staminate inflorescence with 7-20 flowers, corymbiform, up to 7 cm long; pedicels to 5 mm long, red; peduncles to 1 cm long; yellowish pubescence throughout; flowers pinkish, densely pubescent; receptacle obconical; 1 cm long, 8 mm wide; tepals mostly 5-6, 2 mm long, ultimately forming a repand undulate annulus, pink to green streaks, hairs to 0.8 mm long; apical pore 3 mm in diameter; stamens 6, 4 outer 2 inner, separate, whitish, 5 mm long, 2.5 mm wide, clearly exserted; anthers minute, introrse, valvate. Aggregate fruit ecallose, red, globose to subreniform, to 1.5 cm in diameter, moderately to densely pubescent, capped by the minute lobate annulus, bursting irregularly and exposing the pinkish interior and tuberculate seeds. Seeds 5 mm long, gray with black splotches, arillate structure covers the ovary with two lateral lobes, bright red.

This species is very similar to the Peruvian S. hispida but differs in having unequal serrations, long ciliate margins and a rounded base. S. tonduziana may not be distinct from the Ecuadorian S. apicifera. In Panama, S. tonduziana flowers from December-June and has been collected in fruit from Janaury-July. This species occurs from Guatemala to Panama. In Panama, ants are frequently found inhabiting the hollow stems.

BOCAS DEL TORO: In old cemetry, 1.5 mi W of Almirante, Blum 1354 (SCZ). Region of Almirante, Cricamola Valley Cooper 194 (F, NY). Region of Almirante, Buena Vista Camp on Chiriqui Trail 1250 ft, Cooper 596 (F, NY). Rio Teribe between Quebrada Huron and Quebrada Schlunjik, Kirkbride & Duke 489 (NY, SCZ). Cloud forest above Quebrada Huron on Cerro Bonyik 150-360 m, Kirkbride & Duke 616 (NY). Von Wedel 170 (F, GH). COCLE: NE Slopes of Cerro Caracoral, N rim of El Valle, 2700-3200 ft, Sytsma 3751 (F, MO, NY, PMA), 4054 (F, MO, PMA). COMARCA DE SAN BLAS: Vicinity of Summit of Cerro Obu, 2400 ft, Antonio 5375 (F, MO, NY, PMA). PANAMA: Trail to top of Cerro Pelado, 1000 m, Antonio 1105 (F, MO, NY, PMA).

16. Siparuna vinosa T. Antonio, Sp. nov. TYPE: PANAMA, Province of Panama, Vicinity of Cerro Campana, 850 m, Antonio 5294 (MO, holotype; F, PMA, NY, isotypes). __Fig. 30, 31, 32, 33, 34.

Frutex dioecia 1-2.5 m alta; ramulis pilis stellato; folia opposita, obovata vel angusta obovata vel oblanceolata, 7-14 cm longa, 2.5-5 cm lata; integra; apice acuminata vel acuta; basi acuta vel cuneata; petiolo 1-2.5 cm longo. Inflorescentiae feminea pauciflorigerae in axillis foliorum. Flores receptaculo obconico 4-5 mm in diametro tepalis connatis; stylus 10-20; inflorescentiae masculae pauciflorigerae in axillis foliorum. Flores viridis vel luteus, staminibus 6.

Treelet 1-2.5 m tall; dioecious; aromatic; seldom branching from the base, stems and branchlets with tufts of stellate hairs sparse to moderately dense. Leaves opposite, rarely ternate, obovate to narrow obovate rarely oblanceolate, 7-14 (20) cm long, 2.5-5 (7) cm wide; entire; apex acuminate to sometimes acute; base acute to cuneate; 9-13 pairs of lateral veins; pubescence often of stellate hairs, sparse on both upper and lower leaf surface; petioles 1-2.5 cm long, opposing nearly always of differing lengths, longer up to 1.5 times the length of shorter. Pistillate inflorescence of 2-6 flowered axillary cymes, rarely cauliflorous; pedicels 0.2-0.4 mm long; peduncles 0.3-0.6 mm long; flowers green maturing to pale yellow; stellate pubescence limited to outside receptacle; 4-5 mm in diameter; well developed floral cup; firm obconical; felum usually glabrous; tepals connate forming a margin with the velum and the floral receptacle which is undulate; apical pore 1-1.2 mm in diameter; styles 10-20, separate, exserted through aperture-like pore, filiform, 2 mm long; stigmas club shaped, ca. 1 mm long. Staminate inflorescence of 2-8 flowered axillary cymes, peduncles 0.3-0.6 mm long, rarely cauliflorous, similar to pubescence and shape to the pistillate flowers, more flowers per inflorescence and more per similar sized individuals than pistillate plants; velum appears more conical due to upward pressure of emerging stamens; apical pore 1-1.2 mm in diameter; stamens 6, 4 outer and 2 inner, 2 mm long, filaments dilated, 1 mm wide; anthers minute, valvate, opening with 2 flaps, introrse, usually exserted. Aggregate fruit ecallose, globose, 1-1.7 cm in diameter when mature, capped by a persistent green annulus, burgundy to wine red, stellate pubescence sparce, bursting irregularly exposing a red to deep red interior with 2-8 tuberculate seeds. Seeds 5 mm long, gray with black splotches, arillate structures cover the ovary with two lateral lobes and are bright red.

S. vinosa is characterized by its small stature and its abundant deep red fruit (Fig. 33), for which it is named. At present this species is known only from Panama. S. vinosa differs from other species observed in the field, in that it flowers and fruits throughout the entire year (Antonio, 1983).

COCLE: Vicinity of El Cope near Rio Blanco, 1700 ft, Antonio 5371, 5472 (F, MO, PMA, US). Cerro Caracoral, 2700-3200 ft, Dwyer & Correa 9833 (F). Continental divide 4 mi past Llano Grande on road to Cascajal, NW of Penonome, 500 m, Sytsma 3883 (MO). COLON: Vicinity of Guasimo on Rio

Miguel de la Borda, Croat 9998 (US). DARIEN: S slope of western most peak of Tacarcuna massif, above Rio Pucuro, 800-1200 m, Gentry 16961 (NY). PANAMA: Along trail to top of Cerro Pelado, 1075 m, Antonio 1075 (F, MO, PMA). Cerro Campana cloud forest 850 m, Antonio 5292, 5295 (MO). Trail to top of Cero Campana, Correa & Dressler 290 (PMA). Cerro Campana, moist forest on slope near FSU bulding, Croat 12138 (US), 22797 (NY). Cerro Campana, 500-1000 m, D'Arcy & Sytsma 14635 (MO). Cerro Campana area 3000 ft, Dwyer & Weaver 11281, 11308 (DUKE). Cerro Campana cloud forest, 800 m, Kennedy 328, 356 (WIN), 489 (DUKE, US). Upper slopes of Cerro Campana, 207 m, LeDoux 2576 (CAS). Cerro Campana cloud forest, Luteyn & Kennedy 1792 (DUKE, F, GH) 1811 (DUKE, F). Summit of erro Campana, Madison 769 (GH). Cerro Campana near Motel Su Lin, Mendez 145 (PMA). Cerro Campana, low cloud forest near the summit, Smith 3355 (F). Santa Rita hills, cut over secondary forest, Smith 3443 (F, US). Vicinity of Cerro Campana, 2500-2900 ft, Utley 5704 (DUKE). Cerro Campana moist forest, 2000 ft, Weaver & Fpster 1686, 1689 (DUKE). Slopes of Cerro Campana, 2700 ft, Wilbur & Weaver 11281, 11308 (DUKE).

EXCLUDED SPECIES: Pittier 5404 (US) originally identified by Standley as S. griseo-flavescens does not fit the original description by Perkins for that species. Specimens previously identified as S. griseo-flavescens have for the most part been named S. vinosa. Because of its very long petioles, dense slender stellate trichomes, dense pubescence on the receptacle of the flower, and styles which appear united at the base, this specimen does not fit into S. vinosa. There is not enough material of the species to warrant naming of a new species until fruiting material and staminate material are available.

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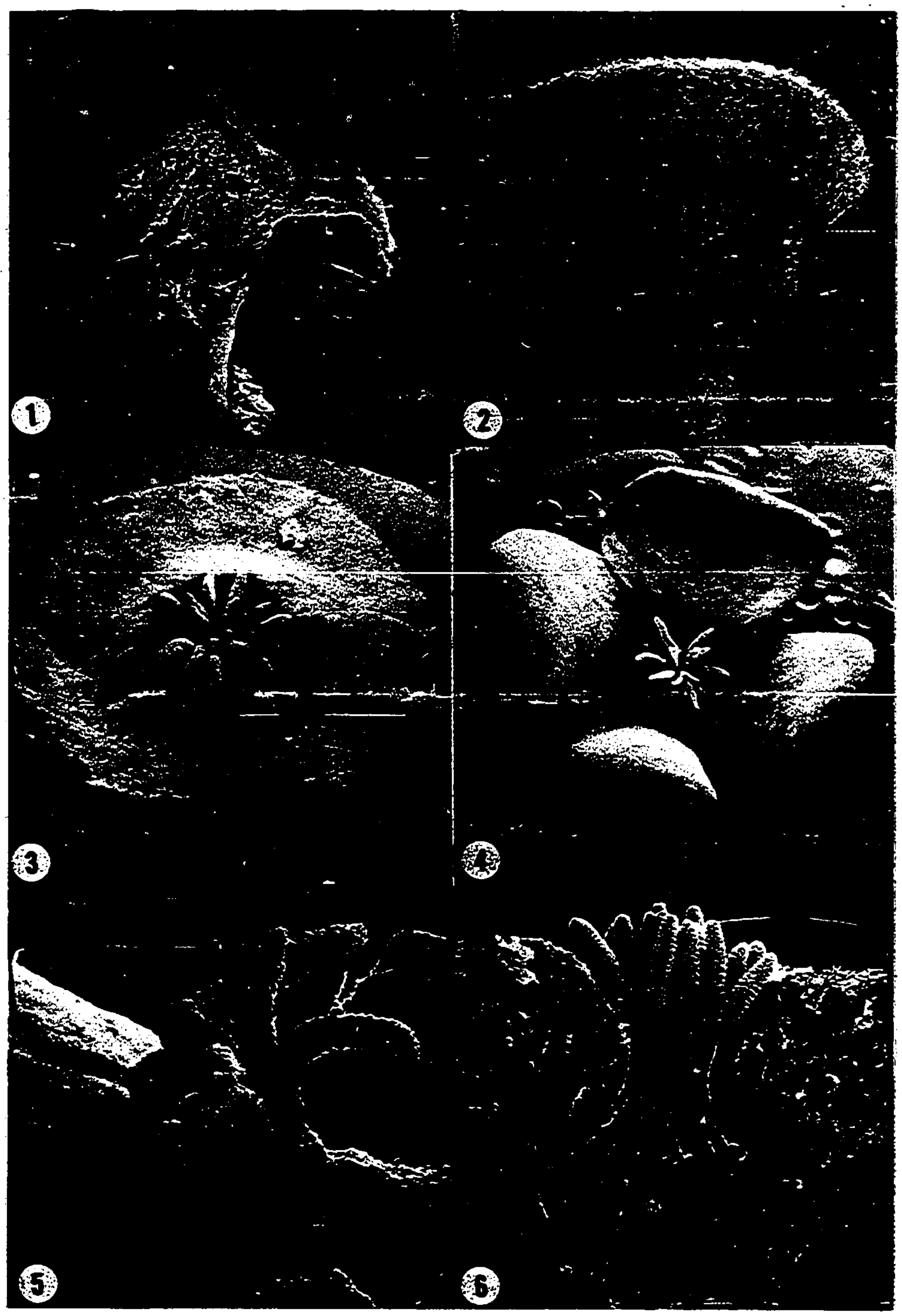
TABLE 1. Comparison of various ordinal placements of Monimiaceae.

Hutchinson 1959 Laurales	Buchheim 1964 Magnoliales	Sastri 1969 Ranales	Takhtajan 1969 Laurales	Thorne 1974 Annonales	Cronquist 1981 Laurales
Austrobaileyaceae	Amborellaceae	Annonaceae	Amborellaceae	Amborellaceae	Amborellaceae
Gomortegaceae	Annonaceae	Berberidaceae	Austobaileyaceae	Annonaceae	Calycanthaceae
Hernandiaceae	Austrobaileyaceae	Calycanthaceae	Calycanthaceae	Aristolochiaceae	Gomortegaceae
Lauraceae	Calycanthaceae	Canellaceae	Chloranthaceae	Austobaileyaceae	Hernandiaceae
Monimiaceae	Canellaceae	Ceratophyllaceae	Gomortegaceae	Calycanthaceae	Idiospermaceae
Myristicaceae	Degeneriaceae	Chloranthaceae	Gyrocarpaceae	Canellaceae	Lauraceae
Trimeniaceae	Eupomatiaceae	Circaeasteraceae	Hernandiaceae	Chloranthaceae	Monimiaceae
	Eupteleaceae	Crossosomataceae	Lactoridaceae	Degeneriaceae	Trimeniaceae
	Gomortegaceae	Dilleniaceae	Lauraceae	Eupomatiaceae	
	Hernandiaceae	Eupomatiaceae	Monimiaceae	Gomortegaceae	
	Himantandraceae	Gomortegaceae	Trimeniaceae	Hernandiaceae	
	Illiciaceae	Gyrocarpaceae		Himantandraceae	
	Lauraceae	Hernandiaceae		Illiciaceae	
	Magnoliaceae	Illiciaceae		Lactoridaceae	
	Monimiaceae	Lardizabalaceae		Lauraceae	
	Myristicaceae	Lauraceae		Magnoliaceae	
	Schisandraceae	Magnoliaceae		Monimiaceae	
	Tetracentraceae	Menispermaceae		Myristicaceae	
	Trimeniaceae	Monimiaceae		Piperaceae	
	Trochodendraceae	Myristicaceae		Saururaceae	
	Winteraceae	Nymphaeaceae		Schisandraceae	
		Paeoniaceae		Trimeniaceae	
		Ranunculaceae		Winteraceae	
		Schisandraceae			
		Winteraceae			

TABLE 2. Chronological list of various divisions within Monimiaceae (* indicates location of *Siparuna*).

<u>Tulasne 1855</u>	<u>Pax 1888</u>	<u>Money et al, 1950</u>
Amboreae	Monimioideae	Hortonioideae
Monimieae*	Hortonieae	Atherospermoideae
Atherospermeae	Hedycarieae	Monimioideae
<u>Baillon 1868-70</u>	Monimieae	Siparunoideae*
Calyrcntheae	Atherospermoideae	<u>Buchheim 1964</u>
Hortonieae	Laurelieae	Hortonioideae
Tambourisseae*	Atherospermeae	Atherospermatoideae
Atherospermeae	Siparuneae*	Monimiodeae
Gomortegeae	<u>Perkins and Gilg 1901</u>	Hedycaryeae
<u>Bentham and Hooker 1883</u>	Monimioideae	Mollinedieae
Monimieae*	Hortonieae	Monimieae
Atherospermeae	Trimenieae	Siparunoideae*
	Mollinedieae	<u>Thorne 1974</u>
	Monimieae	Mollinedioideae
	Atherospermoideae	Atherospermatoideae
	Laurelieae	Siparunoideae*
	Siparuneae*	

FIGURES 1-6.__1. Siparuna tonduziana; pistillate flower (X 9).__2. S. pauciflora; pistillate floral cup (X 9).__3. S. vinosa; pistillate flower with inconspicuous tepals (X 16).__4. S. nicaraguensis; pistillate flower with four conspicuous tepals (X 9).__5. S. nicaraguensis; styles protruding out of apical pore (X 35).__6. S. pauciflora; carpels positioned in wall of hypanthium (X 9).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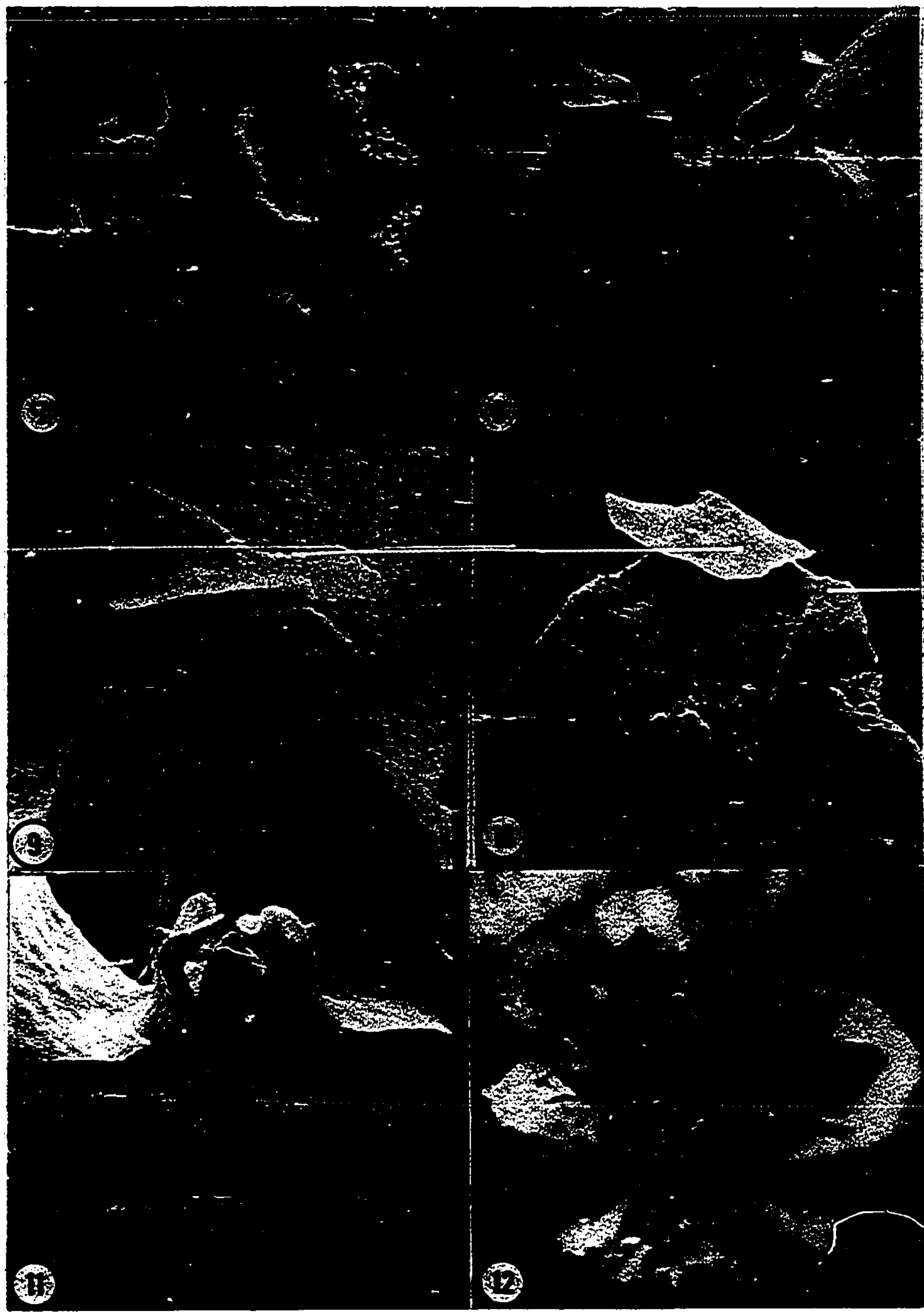
FIGURES 7-12.__7. Siparuna pauciflora; 10-12 stamens (X 35).__8. S. nicaraguensis; 6 stamens 1 removed (X 18).__9. S. nicaraguensis; 2 locular anther (X 43).__10. S. nicaraguensis; anther with one valve flap (X 30).__11. S. nicaraguensis; median section of staminate flower. Note that stamens are not embedded in inner surface of the floral cup (X 25).__12. S. darienensis; floral cup splitting open (X 3).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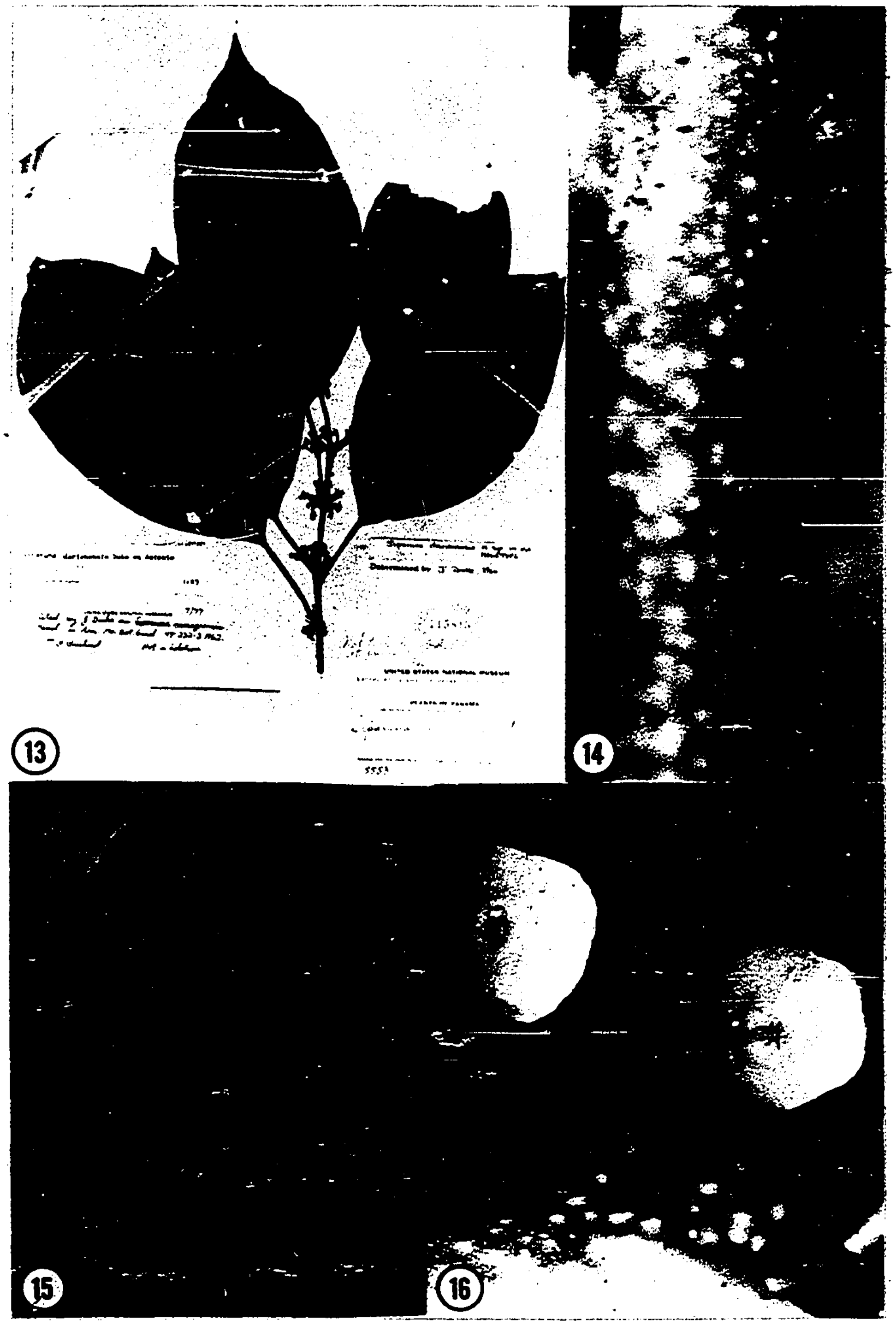
FIGURES 13-16.__13. Siparuna darienensis; holotype (X 1/4).__14. S. darienensis; stem with conspicuous lenticels (X 3).__15. S. darienensis; flowers in axillary cymes (X 1/4).__16. S. darienensis; pistillate flowers with margins of velum reflexed (X 5).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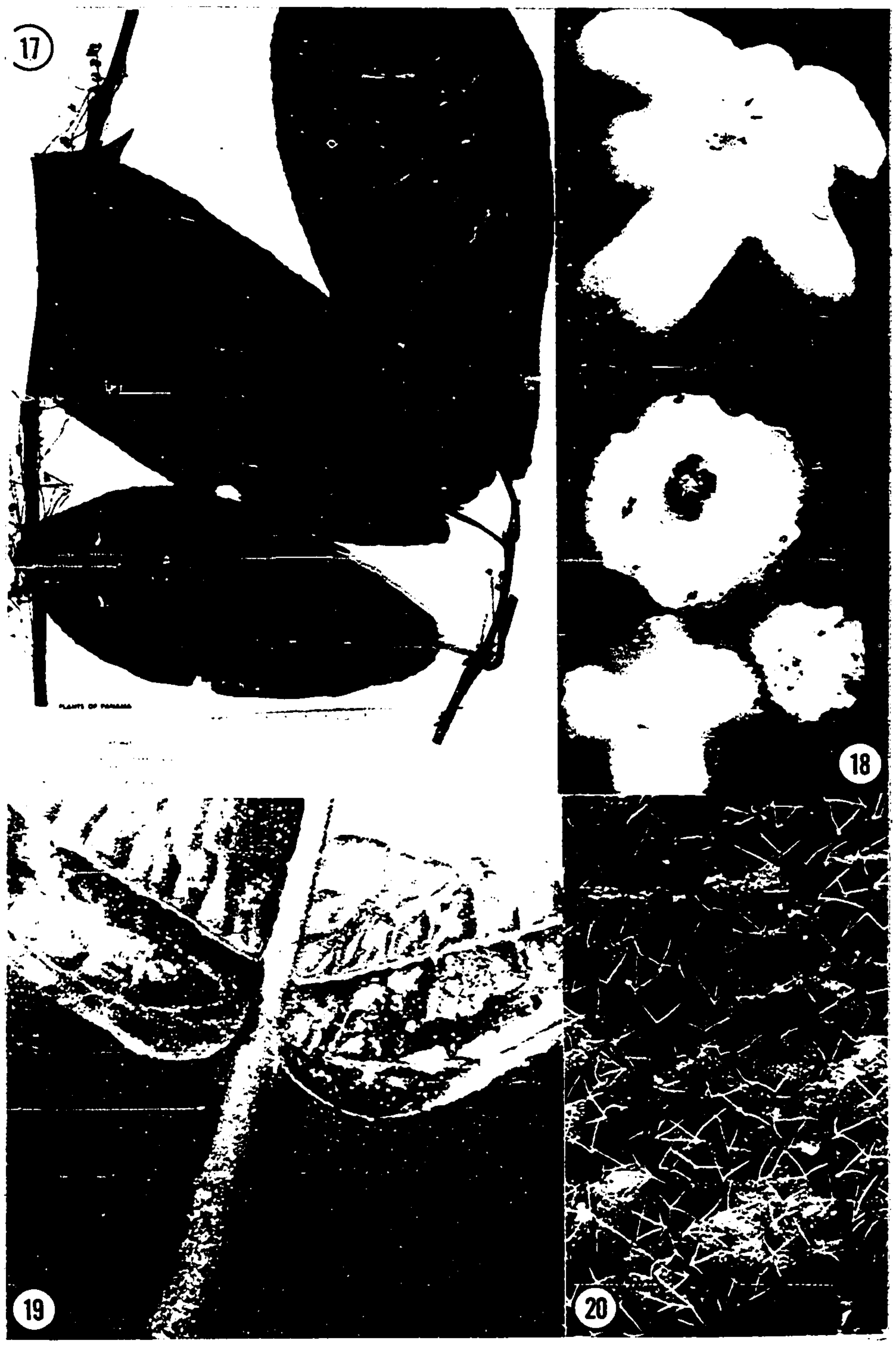
FIGURES 17-20.__17. Siparuna dressleriana; holotype (X 1/4).__18. S. dressleriana; upper a pistillate flower, lower a staminate flower (X 8).__19. S. dressleriana; auriculate leaf base (X 1.5).__20. S. dressleriana; lower leaf surface with stellate hairs (X 1.5).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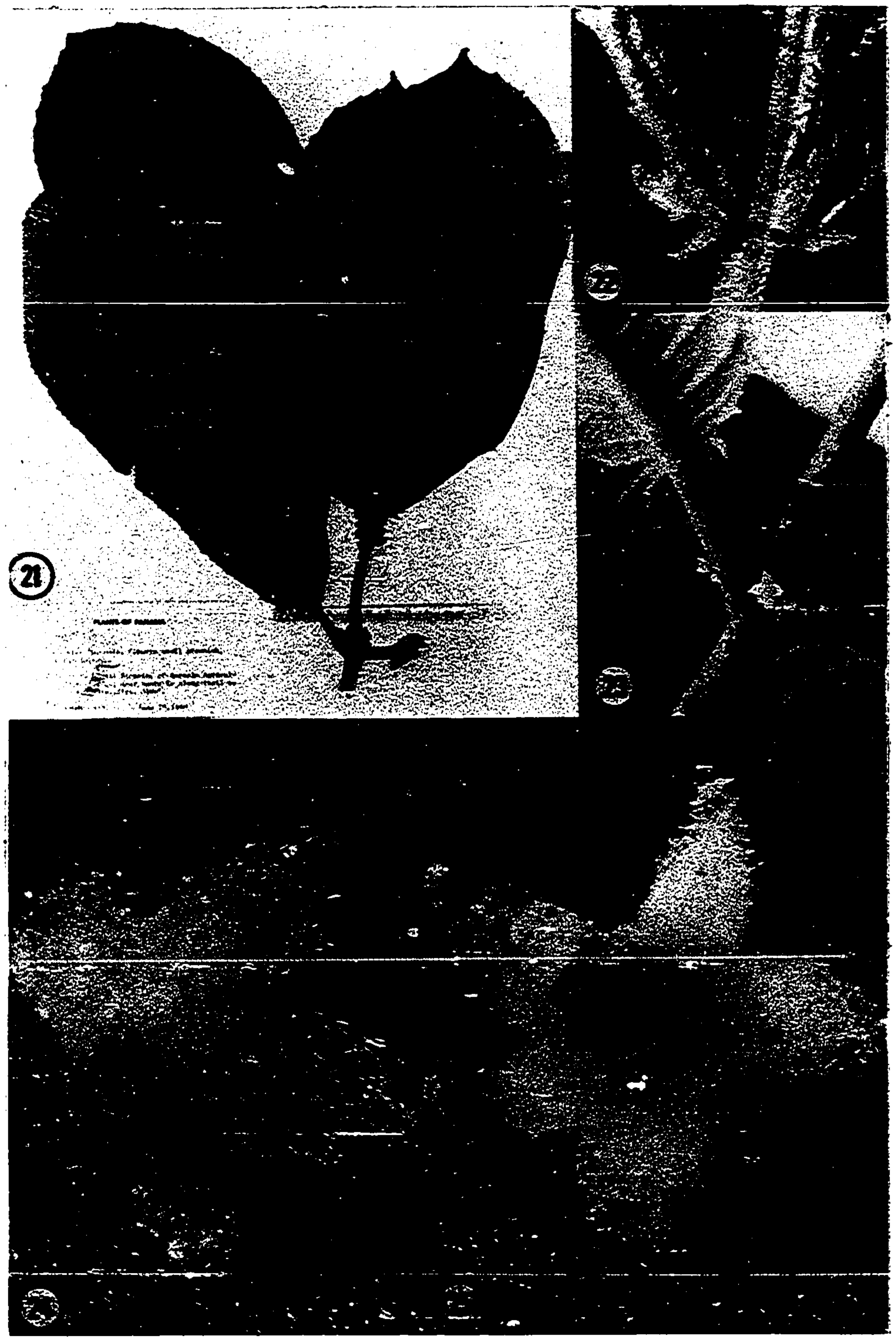
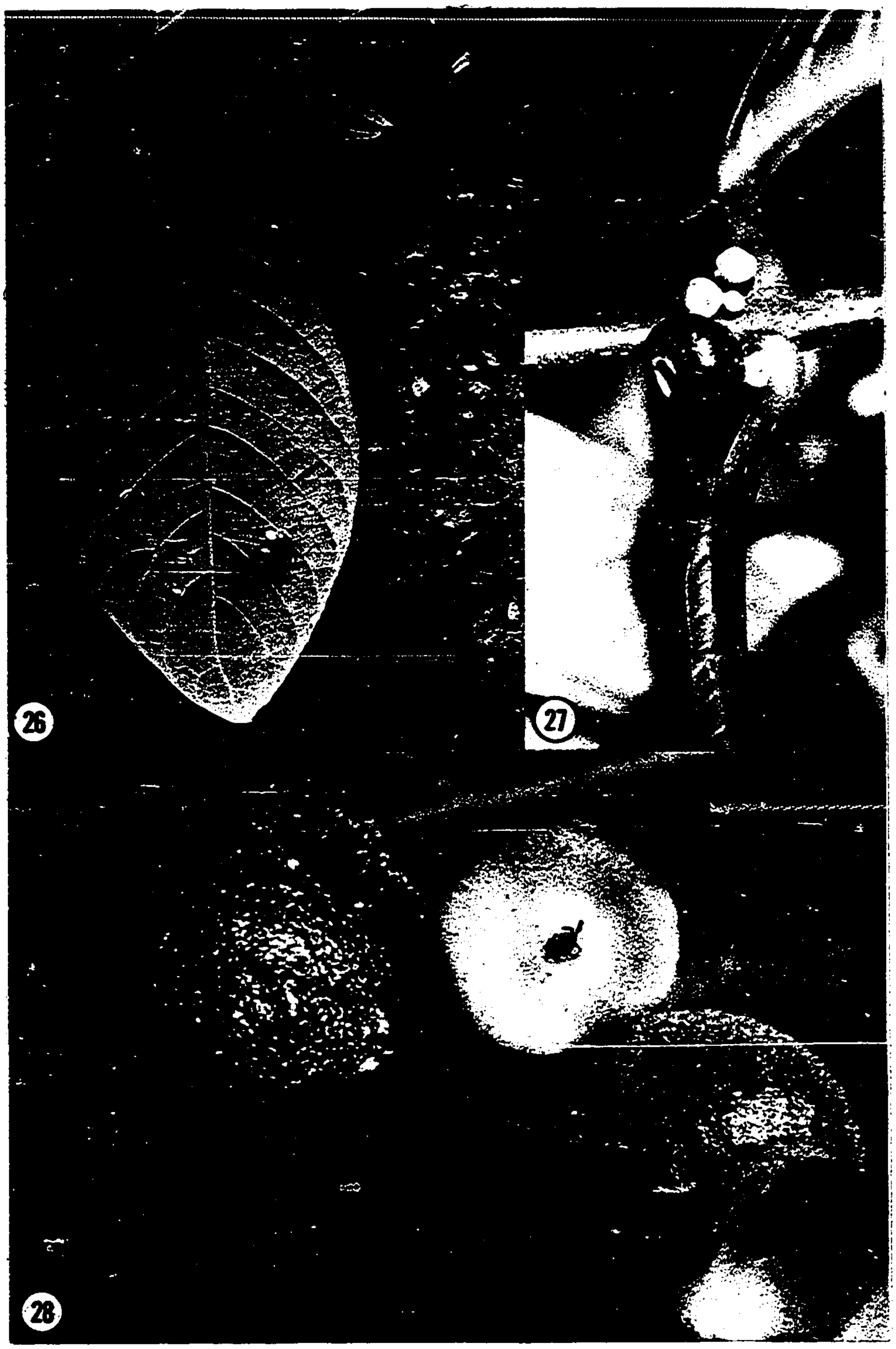
FIGURES 21-25.__21. Siparuna fimbriata; holotype (X 1/4).__22. S. fimbriata; leaf base with fringed appendages (X 1.2).__23. S. fimbriata; flowers borne in leaf axil (X 1/2).__24. S. fimbriata; pistillate flower (X 9).__25. S. fimbriata; staminate flower (X 9).



FIGURES 26-28.__26. *Siparuna rosicosta*; adult leaf (X 1/4).__27. *S. rosicosta*; fruit and flowers in leaf axil (X 1/2).__28. *S. rosicosta*; pistillate flower in center flanked by maturing fruit (X 7).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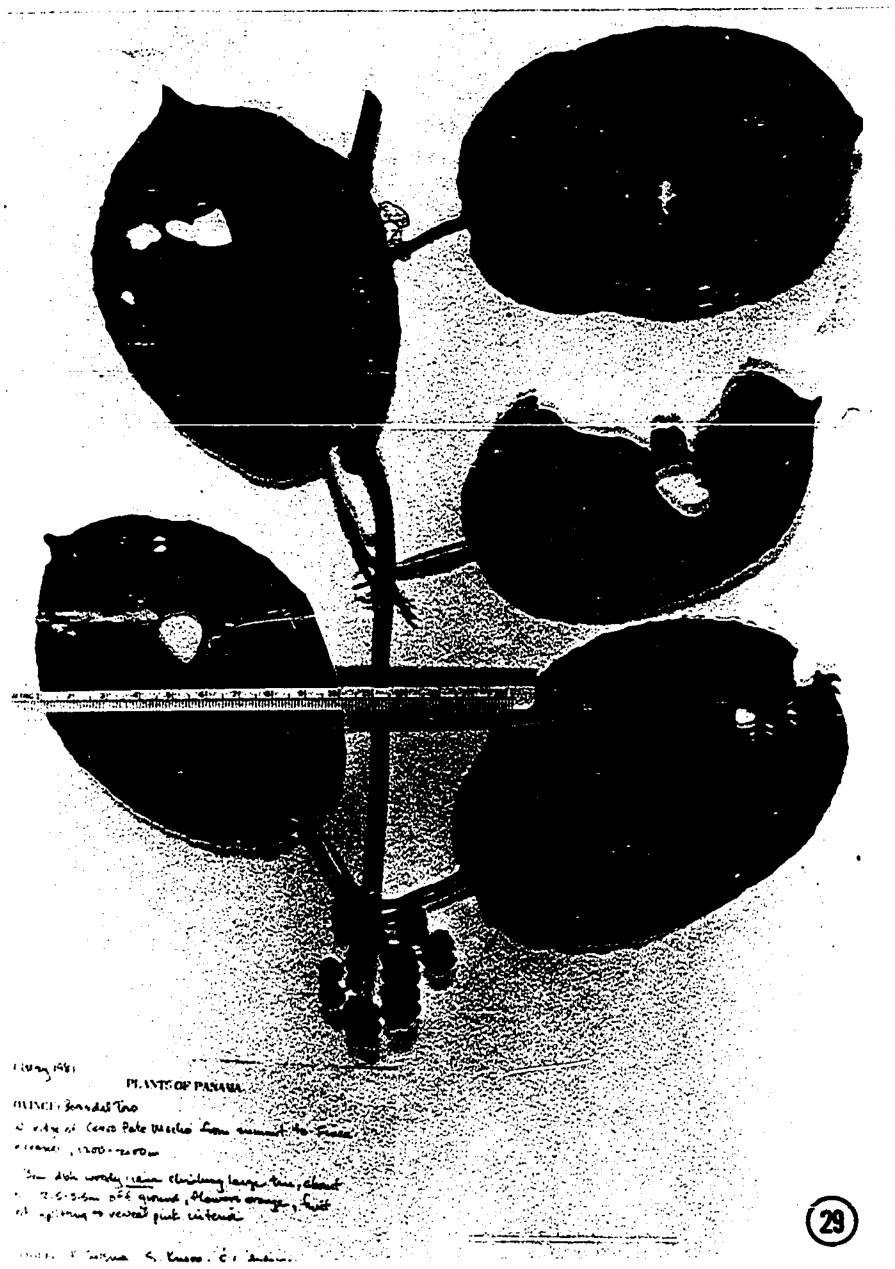
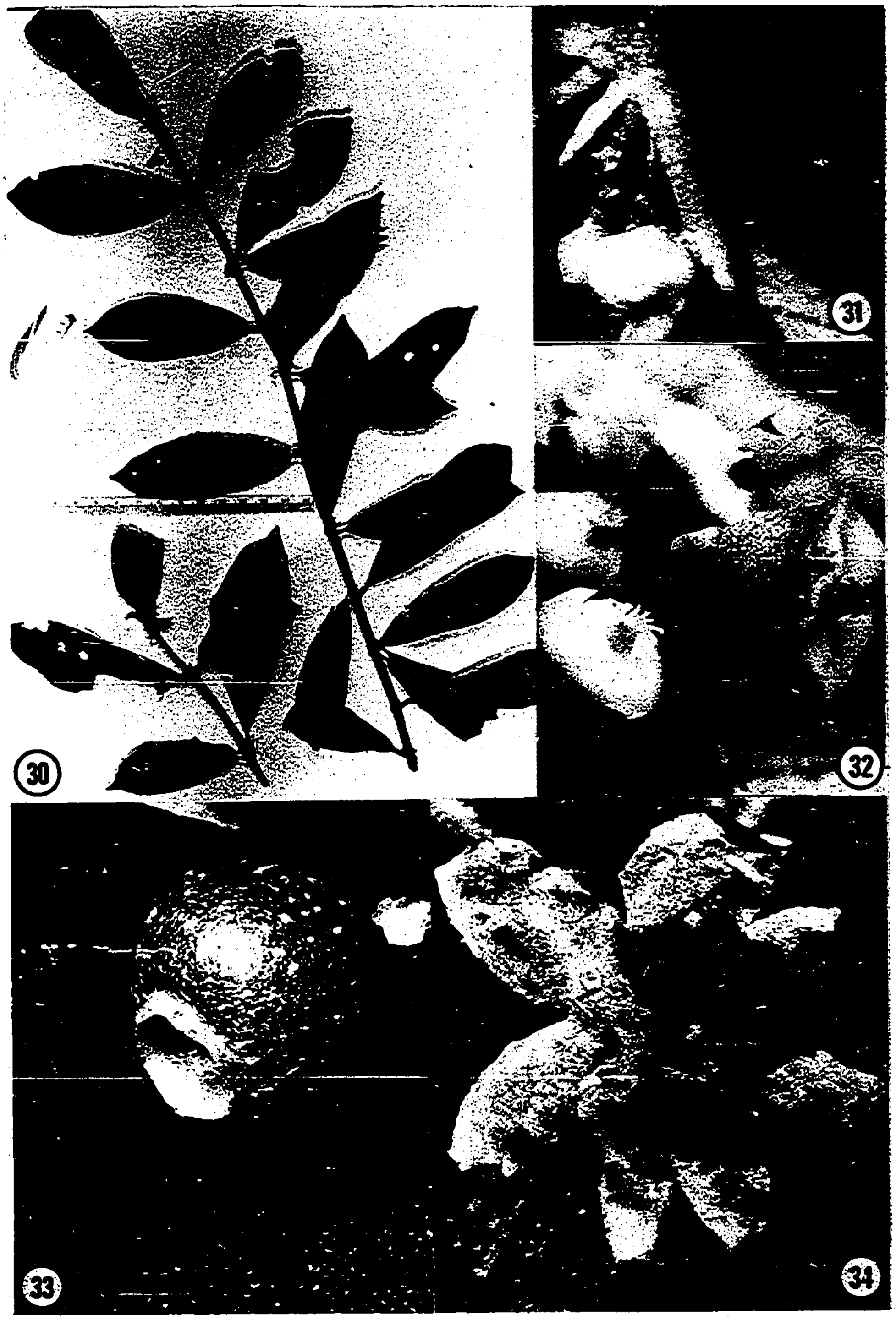
FIGURES 29.__Holotype of Siparuna sytsmania, Sytsma 4899. Note suborbiculate leaf shape (X 1/3).



FIGURES 30-34.__30. Siparuna vinosa; holotype (X 1/4).__31. S. vinosa; staminate flower (X 3).__32. S. vinosa; pistillate flowers (X 4).__33. S. vinosa; mature fruit (X 2).__34. S. vinosa; fruit opening to display arillate seed (X 2).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Phenological and Spatial Relationships Among Three Dioecious Species of Siparuna (Monimiaceae) in Panama

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ABSTRACT

Three dioecious species of Siparuna occur sympatrically in the premontane wet forests of Panama. The two tree species, S. pauciflora and S. nicaraguensis, have seasonal patterns of flowering and fruiting with flowering coincident with the end of the dry season and fruiting peaks at the beginning of the rainy season. Siparuna vinosa, a shrub, is aseasonal in both flowering and fruiting. No patterns of spatial segregation were observed in S. pauciflora or S. nicaraguensis; however, S. vinosa tended to be aggregated. Plants such as S. vinosa with few flowers may increase the probability of seed set by flowering over a longer period of time and by also occurring in aggregate. A longer fruiting period also increases the probability of seed dispersal.

INTRODUCTION

Dioecy occurs in approximately 4% of all species of angiosperms (Yampolsky and Yampolsky 1922); however, the percentage is two to three times higher for tropical dioecious trees (Bawa and Opler 1975). Dioecy is positively correlated with an arborescent habit and there is also a positive association between dioecy and fleshy fruits (Bawa, 1980). Both arborescent forms and fleshy fruits are abundant in the tropics. Nevertheless, the phenomenon of dioecy has played an important role in the evolution of tropical species. However, little detailed data on the phenology and the spatial relationships of dioecious trees in the tropics are available (Bawa and Opler 1977, Frankie et al. 1974, Opler et al. 1980).

Siparuna (Monimiaceae) is a genus of small trees and shrubs found only in the Neotropics. Approximately 80% of the species of the genus are dioecious and all have fleshy fruits. Three species of Siparuna co-occur in the highlands of

Panama and, therefore, provide an opportunity to study dioecy in the tropics without the impact of differing environments.

Studying phenological and spatial patterns in dioecious species is important for understanding animal-plant interactions relative to pollination and seed dispersal. Knowing when a species flowers and for how long is critical to determining the pollinator. A knowledge of distance and arrangement of individuals is important to an understanding of flight patterns and consequently pollen and seed dispersal patterns. There are no reports in the literature on pollination or dispersal in Siparuna and in fact, only a few reports of possible pollination syndromes for other genera in Monimiaceae (Endress 1979, Gottsberger 1977). I examined phenology and population structure of three sympatric dioecious species and made observations of flower and fruit in a preliminary analysis of reproduction in Siparuna and to provide comparative data on dioecious trees.

STUDY SITE

This study was conducted at Parque Nacional de Cerro Campana near Capira, Panama Province, Panama (latitude 8° 42' N, longitude 79° 57' W). Elevation at the site is 854 m. The vegetation of the site is premontane wet forest (Holdridge et al. 1971). The immediate area has undergone moderate disturbance with selective cutting of trees. At Cerro Campana the climate is characterized by distinct wet and dry seasons with the dry season beginning near the end of December and lasting until early April. Rainfall averages about 280 cm per year. The most current rainfall data available are for the period 1948-1958 (fig. 1).

Three species of Siparuna occur at the study site. Individuals of S. pauciflora (Beurl.) A.DC., S. nicaraguensis Hemsl., and S. vinosa Antonio (voucher specimens deposited at MO) were studied in an area of approximately 4 ha. All three species grow in close proximity and no habitat differences were evident. Observations were made from 20 June 1980 to 15 January 1981 and from 15 to 20 March 1981.

PHENOLOGY

A monthly census of the reproductive state of approximately 40 randomly selected staminate and 40 randomly selected pistillate individuals of each species was recorded. Included in the census were the total number of flowers, immature fruits, and open fruits. Fruits which have split to reveal gray seeds with bright red arils (fig. 3D) were characterized as open.

Flowering in S. pauciflora commences in early December with the staminate plants approximately a month before the pistillate plants, and reaches its peak at the end of the dry season (fig. 2A). Peak fruit production occurs in mid-summer (fig. 2A), which coincides with the wet season. The number of open fruits peaks in the late rainy season during November (fig. 2D). Presentation of flowers and fruits had ceased by the end of the rainy season.

The pattern of flower production for S. nicaraguensis is similar to that of S. pauciflora. Flowering also begins on staminate plants early in December about a month before the pistillate plants flower (fig. 2B), and reaches its peak near the end of dry season. S. nicaraguensis also has its peak fruit production in July (fig. 2B), which coincides with the wet season. Near the end of rainy season, a peak in the number of open fruits occurs (fig. 2E).

Flower production for pistillate plants of S. vinosa is relatively constant throughout much of the year (fig. 2C). Staminate production shows a steady decrease into the dry season and then an increase at the beginning of the rainy season; this increase is not as prominent for pistillate individuals. Fruit production is highest in July (fig. 2C), but the number of open fruits on S. vinosa shows only moderate fluctuation (fig. 2F). At any one time during the year this species is in flower and fruit. Thus, flowering and fruiting in S. vinosa is aseasonal.

POPULATION STRUCTURE

All three species of Siparuna that occur at Cerro Campana are different morphologically. The mean heights are: S. pauciflora 4.02 m (SD = 0.79, n = 82), S. nicaraguensis 2.94 m (SD = 1.03, n = 75), and S. vinosa 1.46 m (SD = 0.58, n = 78). A Duncan's multiple range test indicates each species is significantly different from the others ($F = 195$, $P < 0.001$).

The distance was measured between pistillate-staminate (p-s), staminate-staminate (s-s), and pistillate-pistillate (p-p) individuals for all three species. An analysis of variance comparing the p-p, p-s, and s-s distance between species was completed (Table 1). The F-values were all significant. Based on a Duncan's multiple range test of p-p distance, S. vinosa differs significantly from both S. pauciflora and S. nicaraguensis. However, there is no difference between S. pauciflora and S. nicaraguensis. Comparing the s-p distance, S. vinosa was again different from both the other two species, but S. pauciflora and S. nicaraguensis were not different from each other. Finally, in the s-s distance, the only significant difference is between S. vinosa and S. nicaraguensis. The mean distances for p-p, p-s, and s-s for the three species of Siparuna are also given in Table 1. An analysis of variance indicates that within a species there is no difference in the distances for p-p, p-s, and s-s.

To determine if there are size differences between staminate and pistillate plants, an analysis of variance of stem diameter and plant height for each species was completed (Table 1). There is no significant difference in size between staminate and pistillate plants for any of the three species.

The number of flowers on staminate plants of each of the three species was compared with the number of flowers on pistillate plants. Individual flowers were counted on each tree. Staminate plants were paired with pistillate individuals nearest to one another in size and location to reduce the influence of size and habitat. The number of flowers on staminate individuals of S. pauciflora average 1,180 (SD = 1009, n = 10) and the number on pistillate plants average 466 (SD = 628, n = 10). Flowers on staminate individuals of S. nicaraguensis average 561 (SD = 384, n = 10) and on pistillate individuals an average of 155 (SD = 107, n = 10). The smaller species S. vinosa has an average of 173 (SD = 145, n = 10) flowers for the staminate plants and 53 (SD = 39, n = 10) flowers for the pistillate plants. A paired comparisons test (Sokal and Rohlf 1969) demonstrates that all three species produce significantly more staminate than pistillate flowers (S. pauciflora, $t = 3.58$, $P < 0.01$; S. nicaraguensis, $t = 3.50$, $P < 0.01$; S. vinosa, $t = 3.00$, $P < 0.05$).

The number of fruits on a pistillate plant was compared to the distance from its nearest staminate plant by regression analysis (Steel and Torrie 1960). S. pauciflora had a r^2 value of 0.11 and a mean distance of 3.11 m. Distance when compared to number of fruits for S. nicaraguensis resulted in an r^2 of 0.19 and a mean distance of 2.88 m. The shrub species, S. vinosa, had an r^2 value of 0.03 and a mean distance of 0.81 m. There is, therefore, no relationship between the number of fruits on a pistillate plant and its distance from the nearest staminate individual.

To determine if the plants displayed any spatial segregation, Pielou's (1961) nearest neighbor method was used to analyze the dispersion of staminate (s) and pistillate (p) Siparuna. Following Levin (1974) for each species, each staminate (s) and pistillate (p) plant at the site was recorded. The frequency of s-s, p-p, and p-s pairs was scored. A 2 X 2 contingency was used to compare observed and expected frequency of each of the four types of nearest neighbor combinations. Chi-square values were then calculated. The chi-square test was used to test for the hypothesis that the sexes are randomly distributed. In S. pauciflora and S. nicaraguensis, the observed frequencies of s-s, s-p, p-p, and p-s are not significantly different from that expected on the basis of random distribution (Table 3). Thus, for these two species the plants are randomly distributed, with no indication that the sexes are significantly associated. However, S. vinosa plants tend to be aggregated (Table 3). The significant segregation of the sexes for S. vinosa might suggest cloning. Excavations of tree roots revealed that on occasion root suckers are evident.

POLLINATION

Siparuna flowers are borne in axillary cymes and are 4-6 mm in diameter. The species have flowers that are typical of insect pollinated, tropical, dioecious species described by Bawa (1980): small (fig. 3A, B), unspecialized, and usually pale yellow or pale green. The flowers are also radially symmetrical, possess a well developed floral cup, and include a velum (Endress 1980) with an aperture-like pore. The pollen is 12-18 µ in diameter and each staminate flower produces only about 100 grains per anther. No nectar was obtained when samples were taken with a micropipette. The possibility of wind pollination is minimal because: the small amount of pollen produced, stamens sunken into the floral receptacle, and anthers barely exserted out of the flower.

Observations for possible pollinators were made each morning at 0700-1000 hr and each afternoon at 1300-1600 hr during peak periods of flowering for each species. Observations were not conducted during the evenings which were generally very moist with flowers, covered with water and thus, conditions were not conducive for pollen transfer. A total of approximately 340 hr were spent observing the flowers.

Approximately 40 artifical pollinations were performed by removing pollen from dehiscing anthers with a metal probe and immediately transferring it to the stigmatic surface of a pistillate flower with receptive stigmas. The flowers were then bagged. None of the artificial pollinations resulted in seed set. This could be a result of pollination bags causing increased humidity and higher temperatures around the flower. A variety of bags were used including paper, clear plastic, and nylon mesh. The extremely small flowers may have been damaged while trying to place pollen onto the small, often recessed stigmatic surface. K. S. Bawa (personal communication) reports similar difficulties for other small, tropical, dioecious trees. In addition, immature pistillate flowers were bagged without being pollinated, none of these produced fruit.

Aphids (Aphididae) frequently occur inside both pistillate and staminate flowers (fig. 3C). Occasionally aphids were also observed upon the floral velum.

When flowers of S. vinosa are squeezed, aphids emerge from the apical pore and then fly in approximately 15 min. A preliminary analysis of Siparuna steam-volatile extracts indicates that some members of the genus contain the compounds germacrone and elemene (Antonio 1983). These compounds are similar to known aphid pheromones (Edwards et al. 1973, Bowers et al. 1977), and may function to attract aphids to Siparuna.

SEED DISPERSAL

All three species have small gray elliptical seeds approximately 5 mm long, with bright red arils (Endress 1973) 2-4 mm in length. Fruits of Siparuna burst open irregularly and their arillate seeds are displayed on fleshy receptacles (fig. 4D). The fruit of S. pauciflora averages 25.44 seeds (SD = 9.42, n = 50). Fruits of S. nicaraguensis are similar to S. pauciflora averaging 22.57 seeds per fruit (SD = 7.8, n = 50). S. vinosa averages only 9.74 seeds per fruit (SD = 3.18, n = 50).

Observations of potential seed vectors were made during the length of the study. The olive-striped flycatcher, (Mionectes olivaceus) and the ochre-bellied flycatcher (Pipromorpha oleaginea) were observed eating seeds displayed on fleshy receptacles of S. pauciflora in November. The birds hovered before the fruits and picked off individual seeds, eating a few at a time until all the seeds were removed. Selenidera spectabilis, the yellow-eared toucanet, consumed small immature closed fruits of the same species in late March.

During the peak of fruit fall October to November, netting was placed under a large S. pauciflora to catch falling fruit. Initially there were 720 fruits on the tree. At the end of rainy season nearly 50% of the fruits had fallen unopened. Fruits of different sizes fell from the plant, and all contained what appeared to be viable seed. Germination was attempted with and without the presence of arils, and with and without the seed coat removed, however, none of the seed germinated. A few seedlings of S. pauciflora were observed in the field.

DISCUSSION

Dioecious species typically produce more staminate than pistillate flowers (Bawa 1980). This may occur through the production of greater numbers of staminate plants or more flowers per plant or both. In these three species staminate plants produce significantly more flowers than do pistillate plants. Thus more resources are utilized in floral production in staminate plants than in pistillate ones. Pistillate plants, on the other hand, must allocate resources to fruit production, obviously not required in staminate individuals. However, these differences in resource allocation are not manifested in differences in plant height and stem diameter among any of the three species. In other words, size is not correlated with sex. Thus, either resources were not limiting or growth was affected in features I did not measure.

The reproductive characteristics of any plant species represent an evolutionary or adaptive compromise. Siparuna vinosa, the smallest of the three species at Cero Campana has a lengthened period of flowering and fruiting. These two events are not necessarily linked; the selective pressure affecting pollen and seed dispersal are dissimilar (Wheelwright and Orians 1982). Pollen has a specific area, the stigma of a conspecific flower, as a target. In contrast, it is often advantageous for seeds to be dispersed over a wide area. Siparuna vinosa by virtue of its phenological pattern has increased the probability of both successful pollination and seed dispersal. This has been accomplished through increased exposure to pollen and seed vectors.

Opler et al. (1980), in discussing tropical plant phenology, reported that a majority of small trees and shrubs in wet tropical forests were more aseasonal in their flowering and fruiting than were the large trees. These species fit this model; S. pauciflora and S. nicaraguensis (the two larger species) are seasonal and S. vinosa (the smallest of the three species) is aseasonal. Opler (1980) attempted to relate these differing phenological patterns to the greater light and soil moisture available to larger trees. Although rainfall patterns no doubt play an important role in the flowering and fruiting periods of many tropical trees (Janzen 1967, Opler et al. 1976), this does not explain the differences evident among species of Siparuna. All three species experience similar abiotic factors.

A number of other factors may account for the differing patterns for species of Siparuna. Siparuna vinosa is significantly smaller than the other two species of Siparuna, and does not present the large quantities of flower and fruit produced by the other two. It may produce the same number of flowers but over an extended period of time. For instance, S. pauciflora produces up to 10 times more flowers than S. vinosa within the period of time all the species are flowering. In addition, S. pauciflora also produces up to 10 times more fruit. Thus, the interactions of the large and small species of Siparuna with their pollinator and seed vector would differ. I believe it is the interaction with the biotic factors which may account for the observed differences in phenological patterns.

Pollen transfer to the stigmatic surface is necessary for fruit formation, because none of the bagged flowers produced fruit. Aphids were found in and on the flowers of Siparuna. The genus also contains aphid pheromones. Therefore, aphids may play a major role in the pollination of Siparuna. However, aphids are not significant pollinators of other plant groups, do not have hairs on their bodies (Kennedy and Stroyan 1959), and none I saw had pollen on their bodies. In addition, aphids have irregular flight patterns (Kring 1972). They are, nevertheless, the most prominent insect on Siparuna and they do occur in abundance.

In insect-pollinated dioecious plants, distance from the staminate to pistillate is clearly important to the reproductive biology of the species. Pistillate plants located far from a source of pollen could be expected to produce less fruit. In these three species, distance from the nearest staminate plant does not affect the number of fruits produced by the pistillate individuals. This indicates that the pollinators may be very effective.

The bright red aril on the seeds of Siparuna suggests that it is bird dispersed fruit (Van der Pijl 1972). Siparuna fruits have been found in the diets of unspecialized frugivorous birds (Snow 1981). Based on this and the limited number of observations of flycatchers feeding on Siparuna seeds, I infer that Siparuna seeds are probably bird dispersed. Snow (1971) stated that closely related sympatric plant species with unspecialized biotic seed vectors should have similar fruits because selection would set limits of fruit and seed size for the common pool of dispersal agents. All three species may rely upon similar frugivores, because all three have seeds similar in size and color and they are open at the same time. The difference lies in the number of fruits produced. Snow (1971) suggested that natural selection would favor plants that attract the largest number and variety of dispersal agents as do S. pauciflora and S. nicaraguensis. Few seedlings of Siparuna were observed at Cerro Campana. This, coupled with unsuccessful seed germinations, suggests that the seeds may have to pass through the gut of a frugivore to germinate. This is the case with a number of fleshy fruits in the tropics (McKey 1975). Siparuna vinosa with a longer fruiting period has thereby increased the visibility of its fruit.

In addition to longer flowering and fruiting periods, S. vinosa is aggregated. The segregation of the sexes for S. vinosa is reminescent of vegetative reproduction. Excavation of tree roots revealed that on occasion root suckers are evident. Recall that, of the three species, S. vinosa had significantly smaller distances between the sexes than did the other species. The visibility of a few flowers and fruits is increased with aggregation. Siparuna vincsa with a phenological pattern which is aseasonal and an aggregated spatial pattern has increased the probability of pollen and seed dispersal.

ACKNOWLEDGEMENTS

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TABLE 1. Average distance in meters (± SE) between trees of *Siparuna* at Cerro Campana, with sample sizes of distances in parentheses.

Species	n	Pistillate-Pistillate	Pistillate-Staminate	Staminate-Staminate	*F*- values
S. pauciflora	42	2.29 ± 0.41 (14)	3.15 ± 0.52 (22)	1.68 ± 0.32 (6)	1.46 n.s.
S. nicaraguensis	39	2.53 ± 0.44 (13)	2.74 ± 0.42 (21)	1.86 ± 0.37 (5)	0.51 n.s.
S. vinosa	59	0.96 ± 0.10 (22)	0.83 ± 0.07 (21)	0.84 ± 0.16 (16)	0.43 n.s.
n		49	64	27	
F- values		8.42	9.43	3.88	
Probability level		$P < 0.01$	$P < 0.01$	$P < 0.05$	

TABLE 2. Analysis of mean height and stem diameter (± SE) of pistillate and staminate trees.

Species	Height				Diameter			
	Pistillate (m)	Staminate (m)	n	*F*-value	Pistillate (cm)	Staminate (cm)	n	*F*-value
S. pauciflora	4.01 ± 0.09	4.03 ± 0.08	82	0.02	4.48 ± 0.35	4.60 ± 0.35	73	0.12
S. nicaraguensis	2.88 ± 0.13	3.05 ± 0.14	73	0.45	3.12 ± 0.25	2.84 ± 0.25	73	0.55
S. vinosa	1.37 ± 0.08	1.55 ± 0.08	76	1.75	1.26 ± 0.06	1.49 ± 0.06	76	2.22

TABLE 3. Analysis of nearest-neighbor relationships between staminate and pistillate plants of *Siparuna* at Cerro Campana.

Species	Base plant	Nearest neighbor		X^2
		Staminate	Pistillate	
S. pauciflora	Staminate	6	10	0.303
	Pistillate	12	14	
	Total	18	24	
S. nicaraguensis	Staminate	5	10	0.596
	Pistillate	11	13	
	Total	16	23	
S. vinosa	Staminate	16	10	4.661[a]
	Pistillate	11	22	
	Total	27	32	

[a]Significant at $P<0.05$.

FIGURE 1. Mean monthly rainfall at Cerro Campana. 1948-1958. Standard error indicated by vertical bars.

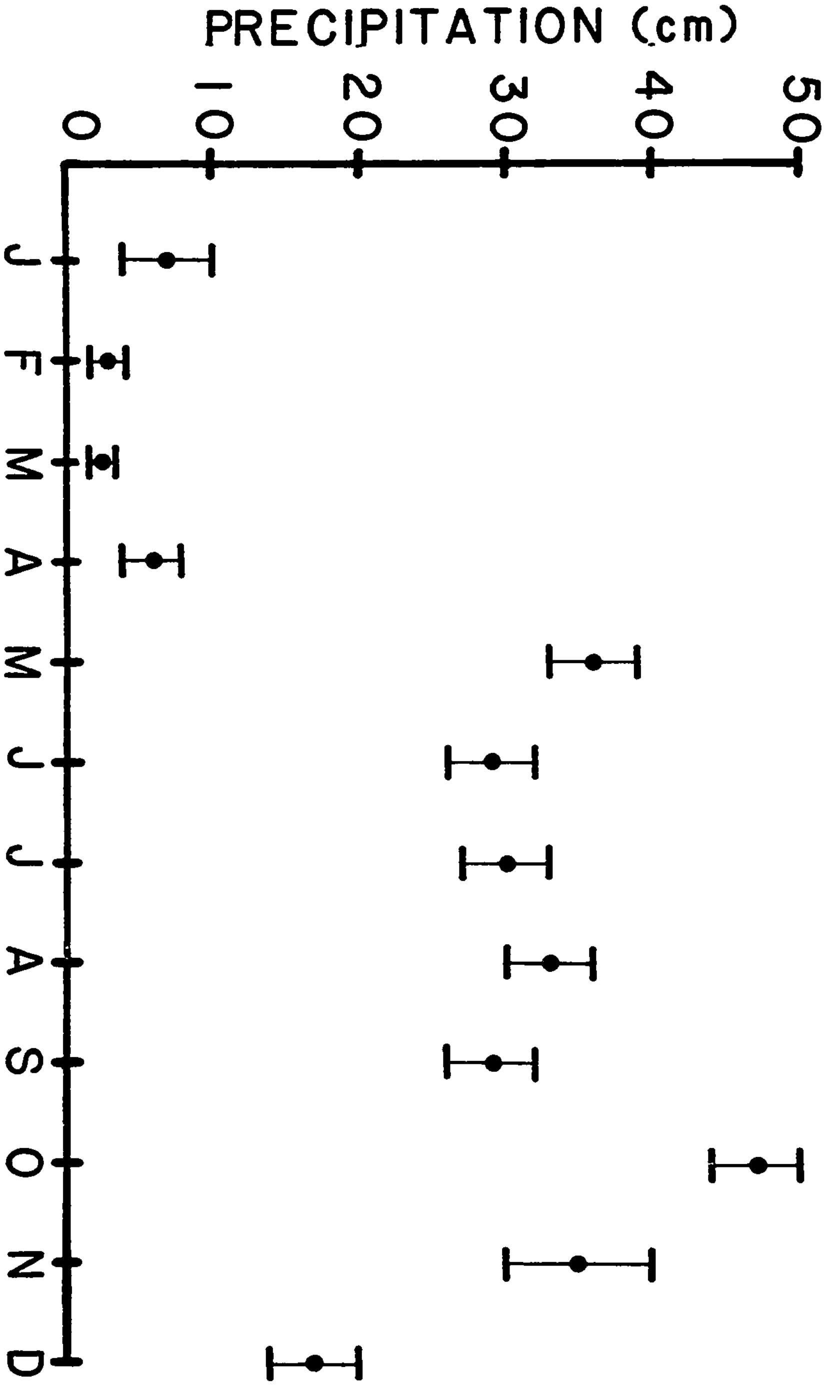
PRECIPITATION (cm)
0
10
20
30
40
50
J
F
M
A
M
J
J
A
S
O
N
D

FIGURE 2. Monthly census of the number of flowers (*) pistillate (♀) and staminate (♂) and fruits (o) of (A) S. pauciflora; (B) S. nicaraguensis; (C) S. vinosa. Number of opened fruits on (D) S. pauciflora; (E) S. nicaraguensis; (F) S. vinosa.

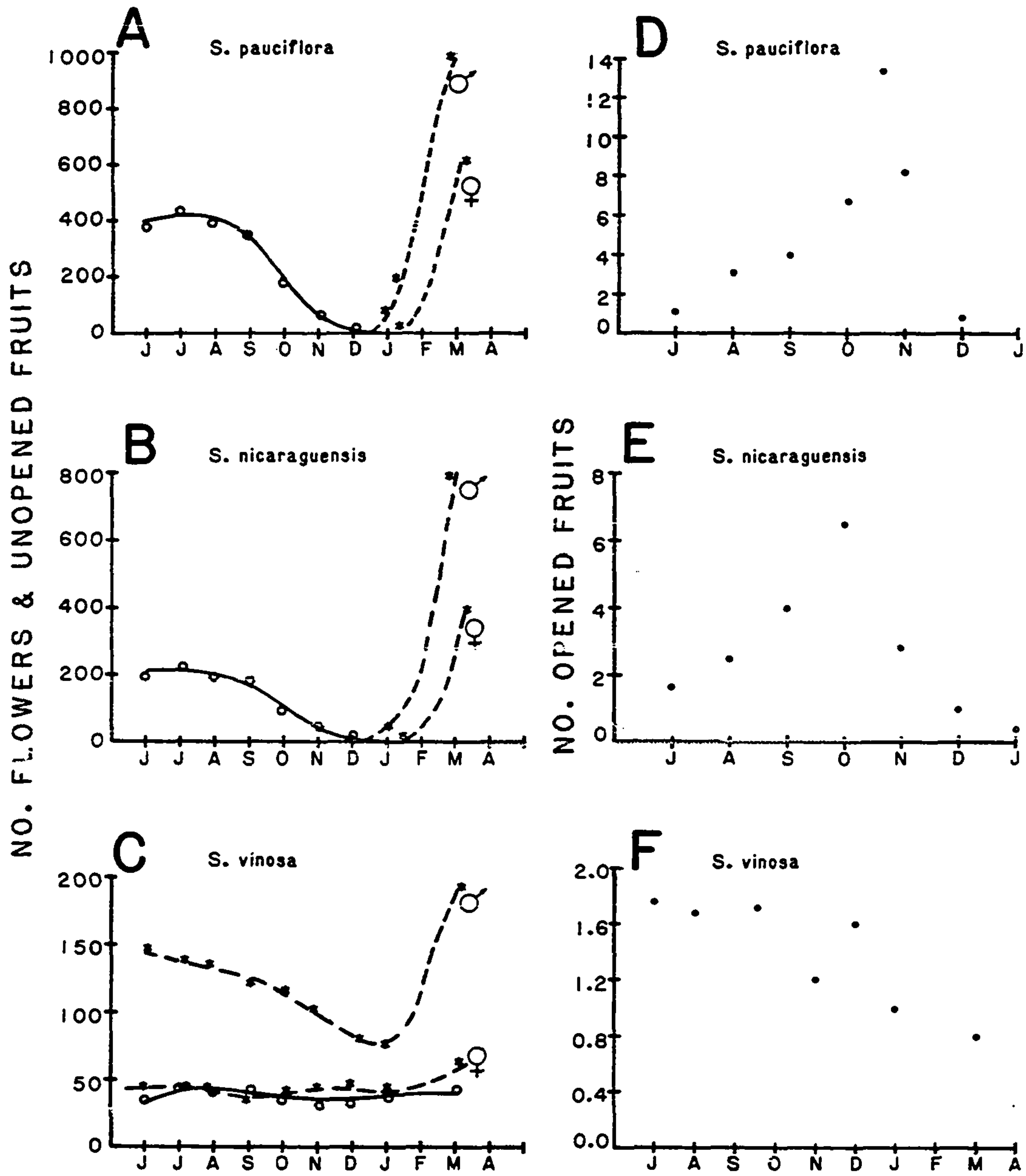
A
S. pauciflora
B
S. nicaraguensis
C
S. vinosa
D
S. pauciflora
E
S. nicaraguensis
F
S. vinosa
NO. FLOWERS & UNOPENED FRUITS
NO. OPENED FRUITS
J J A S O N D J F M A
J A S O N D J
J A S O N D J F M A
1000
800
600
400
200
0
14
12
10
8
6
4
2
0
2.0
1.6
1.2
0.8
0.4
0.0
150
100
50

FIGURE 3. A, pistillate flower of S. vinosa, X 20; B, staminate flower of S. vinosa, X 20; C, aphid from flower of S. vinosa, X 60; dehiscing fruit of S. pauciflora, X 1.5.


A
B
C
D

Monimiaceae. I. Composition of Essential Oil from the Leaves of *Siparuna guianensis*

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Key Word Index: *Siparuna guianensis*: Monimiaceae: Curzerenone: Myristicin

Running head: Essential oil of *Siparuna guianensis*

Abstract

Some components of the essential oil from the leaves of Siparuna guianensis (Monimiaceae) were identified and determined in the steam-volatile extract. The major constituents are curzerenone (26%) and curzerenone types (42%), as well as myristicin or an isomer (8%). This represents the first chemical study of the composition of Siparuna guianensis oil.

Introduction

Siparuna (Monimiaceae) is a genus of small trees or shrubs that occurs only in the Neotropics, ranging from Veracruz, Mexico south through tropical South America. It is characterized by decussate leaves, imperfect flowers, and globose fruits born in the axils of the leaves or on the stems. Foliage and flowers of Siparuna are very aromatic with an odor similar to that of Citrus. In fact, one of the early names applied to the genus was Citrosma.

The Monimiaceae are placed in the order Laurales by Cronquist (1). As such, it is related to Atherospermataceae, Calycanthaceae, and Lauraceae. All these families possess spherical ethereal oil cells in their parenchymatous tissues and are tanniferous. In addition, these families are aromatic. Chemical features, including ethereal oils, have long been of practical value in identification, e.g., Umbelliferae (2) and Magnoliaceae (3). Odor, a function of the volatility of the oils, may also be adaptive in the attraction of pollen vectors (3) or to deter predators (4, 5, 6). The oils are composed mostly of terpenes and terpenoids which contribute to the powerful odors. These compounds are widespread and diverse, thus there is little reason to doubt they have taxonomic potential. In fact, the usefulness of comparative chemistry in plant taxonomy is well documented (7, 8).

Chemical data for Monimiaceae (sensu lato) are sparse. Some of the earliest chemical research on Monimiaceae dealt with the composition of their volatile oils and was summarized by Gildemeister (9). However, only about 8 species in the entire family of some 350 species have been examined chemically. In fact, the survey by Guenther (10) on essential oils does not even mention Monimiaceae. The most complete summary to date of the chemistry of this family is that of Gibbs (11).

More recently Smolenski (12) noted that Siparuna pauciflora contains alkaloids; Braz (13) listed sitosterol, stigmasterol, liriodenine, cassamedine, and fuseine (an oxoaporphine alkaloid) as components of S. guianensis; and Altschul von Reis (14) listed the possible drug uses for Siparuna. Levin (15) reported that 64% of the species tested in Monimiaceae contain alkaloids; but his survey was incomplete.

Other than the biochemical analysis on Lauraceae (16), most families related to Monimiaceae have had little or no chemical analysis; however Atherospermataceae, which have been split from Monimiaceae, have received considerable attention from Urzua and Cassels (17). As in Monimiaceae the leaves and bark of Atherospermataceae are very fragrant.

Aside from the possible taxonomic benefits that chemical analysis of Siparuna may provide, Monimiaceae, and more specifically Siparuna, has a long history in folk medicine. It is reported that Siparuna is used as a stimulant and carminative in Brazil. Indians in Panama drink a tea made from the leaves as a remedy for colds and snakebites. In Guatemala, the Indians place the fresh leaves on the forehead to relieve headache, and the sap that exudes from leaves placed on hot coals is applied to cuts (18). These reported uses need to be substantiated. Analysis of the chemical compounds present in Siparuna may lead to a greater understanding of the potential medicinal properties in this plant. This study was undertaken to provide baseline data that could be used later to address an understanding of plant-animal interactions, taxonomic relationships, and medicinal properties of Siparuna.

Materials and Methods

Steam-volatile extracts were obtained in Panama using freshly collected material. Approximately 700 g of Siparuna guianensis leaf material were collected from randomly selected trees along Pipeline Road, Zona de Canal, Panama at 1000 hr on 29 September 1980. The material was kept cold until the steam distillation began at 2100 hr. The distillation took nearly 2.5 hrs in an all-glass system with no stopcock grease. The distillate was saturated with ACS certified reagent sodium chloride (Baker) and extracted with ethyl ether. The ether solution was dried over anhydrous magnesium sulfate, filetered, and freed of ether and the essential oil stored at 0° C until analyzed.

The extracts were then analyzed by gas chromatography using a Hewlett Packard Series 5880A gas chromatograph equipped with a 50 m x 0.32 mm OV-1 fused silica column. The oven temperature was programmed from 70 to 225° C at 2°/min. The helium flow rate was 1.8 ml/min. GC-MS analysis was subsequently carried out on a Kratos MS 50 mass spectrometer equipped with a Varian Model

3700 gas chromatograph using an OV-1 fused silica column as described above. The data were acquired and analyzed using a Kratos Model DS-55 data system. Identifications were based on the comparison of known and unknown mass spectra and were confirmed whenever possible by I_E values, that is, the retention indices relative to a series of ethyl esters of normal alkanoic acids (19).

Results and Discussion

The GC profile of the essential oil from the leaves of Siparuna guianensis is shown in Figure 1. Of the approximately 110 compounds separated by GC in the essential oil, 30 were identified (Table 1). The major constituent is curzerenone (I; 26%) (Structure I placed here) and curzerenone types (42%), which comprise approximately 68% of the total. The mass spectrum of curzerenone is shown in Figure 2A. Curzerene (II) (Structure II placed here), which comprises only 0.36% of the oil, is probably the precursor to curzerenone and other isomers; if this is so, the plant is very efficient in carrying out the enzymatic oxidation. Figure 2B shows the mass spectrum for curzerene, which, like curzerenone is a sesquiterpenoid. Myristicin (Fig. 3A), also a sesquiterpenoid, is the next major constituent (III; 8%) (Structure III placed here). Myristicin is the most abundant component of the heavy oil of nutmeg, Myristica fragrans (Myristicaceae) (20), and occurs in a number of other essential oils. Germacrone (IV: 0.76%) (Structure IV placed here) and ocimene quintoxide (V; 0.11%) (Structure V placed here) are two compounds about which little is known. Their mass spectra are shown in Figurs 3B and 4A, respectively. Germacrone is a sesquiterpenoid and ocimene quintoxide is a monoterpenoid.

Based on field studies by T. M. Antonio (unpubl. data) the leaves and flowers of each species of Siparuna has its own characteristic odor. We suspect that these odors may prove to be important in the pollination as an attractant, but this has yet to be confirmed. The compound methyleugenol, which had a retention time of 39.08 min (Table 1), is known to be an insect attractant found in many natural sources. Aphids are frequently found in the flowers of Siparuna (21), and germacrone, another constituent of the essential oil, is very similar to germacrene A, a known aphid pheromone (22). The similarity of compounds in the essential oil of the leaves of Siparuna guianensis to those of known aphid pheromones is worthy of further investigation.

Curzerenone, a major component of the Siparuna guianensis essential oil, was originally isolated form Curcuma zedoaria (Zingiberaceae) in which it is the major constituent. This East Indian turmeric plant is used to make the drug zedoary (23, 24). Thus, although there are many reports of the use of Siparuna in folk medicine, the identification of compounds that occur in known drug plants lends support to the possible medicinal applications of Siparuna.

This is the first report of curzerenone, myristicin, germacrone, and ocimene quintoxide in any member of Monimiaceae. These compounds are not known to occur in the closest family to Monimiaceae, Atherospermataceae, nor in other families in the order Laurales. Monimiaceae and Atherospermataceae were separated by Money (25) on the basis of morphological features. Atherospermataceae are characterized by monocolpate pollen, tepals which are petal-like, and stamens with an appendage. In Monimiaceae pollen is acolpate, tepals are reduced, and staminal appendages are lacking. Although some authors do not recognize the separation of these families, this chemical analysis provides some support for Money's separation. Further biochemical research on Siparuna is needed if it is to be useful in determining taxonomic relationships with other members of Monimiaceae, in elucidating possible medicinal uses, and in helping to understand the pollination.

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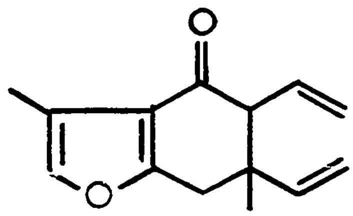

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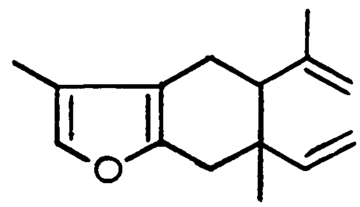

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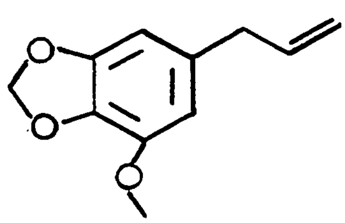

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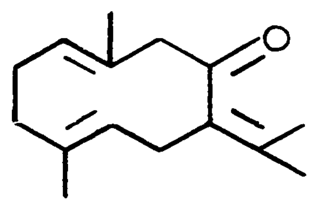

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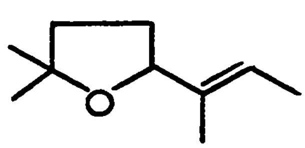


(V)

Fig. 1. The GC profile of the essential oil from the leaves of Siparuna guianensis.

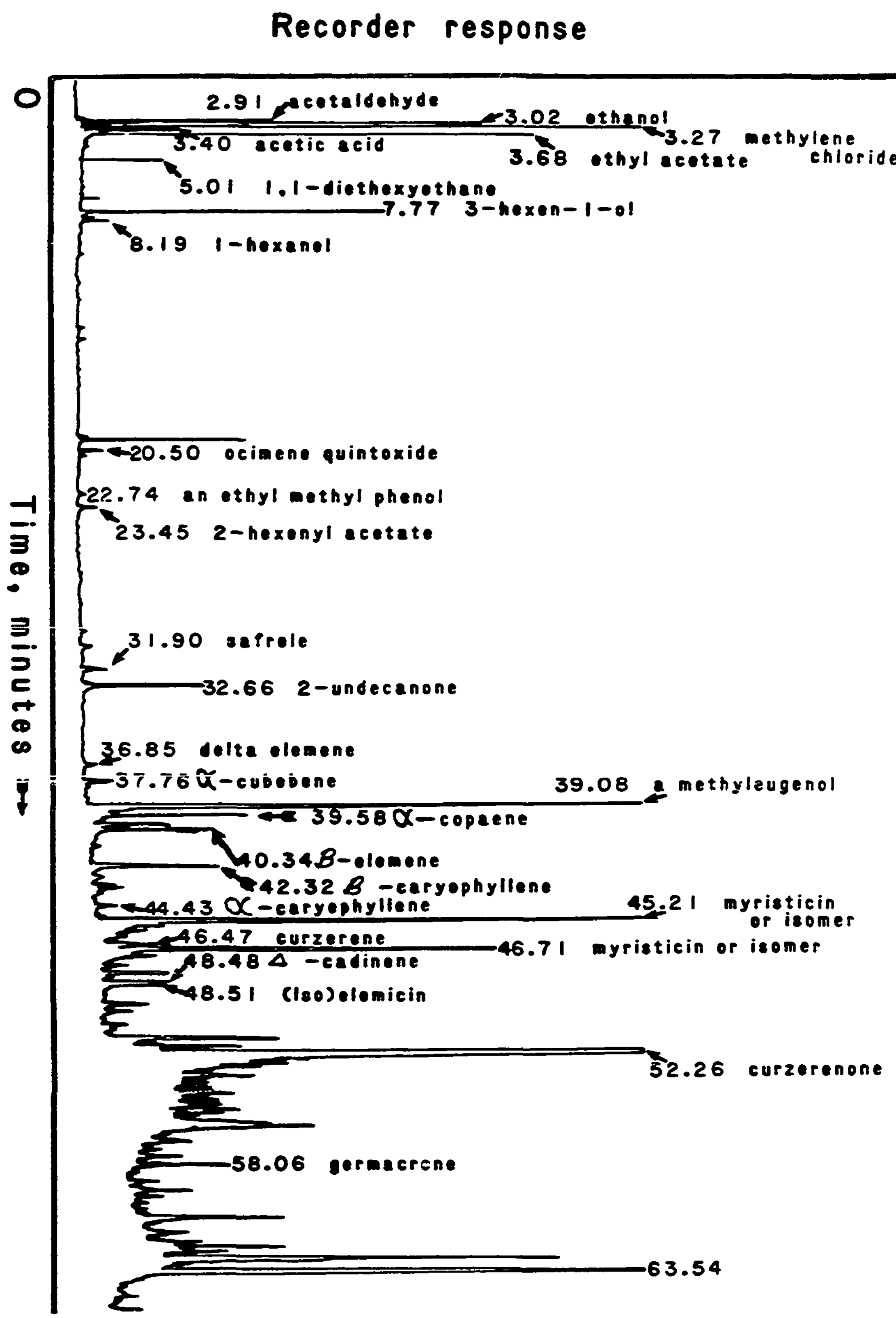
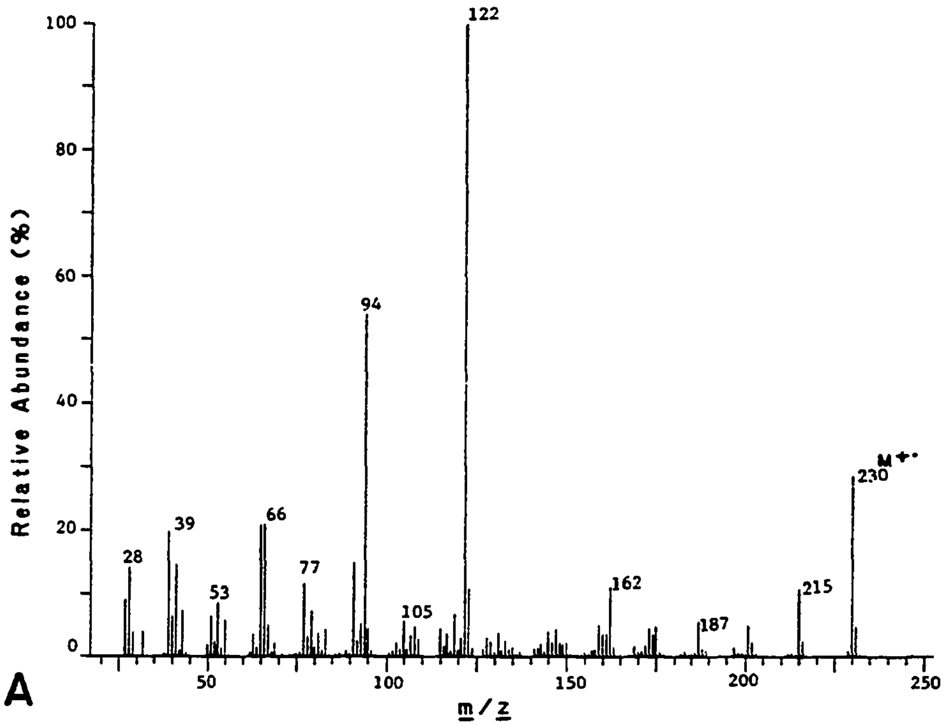
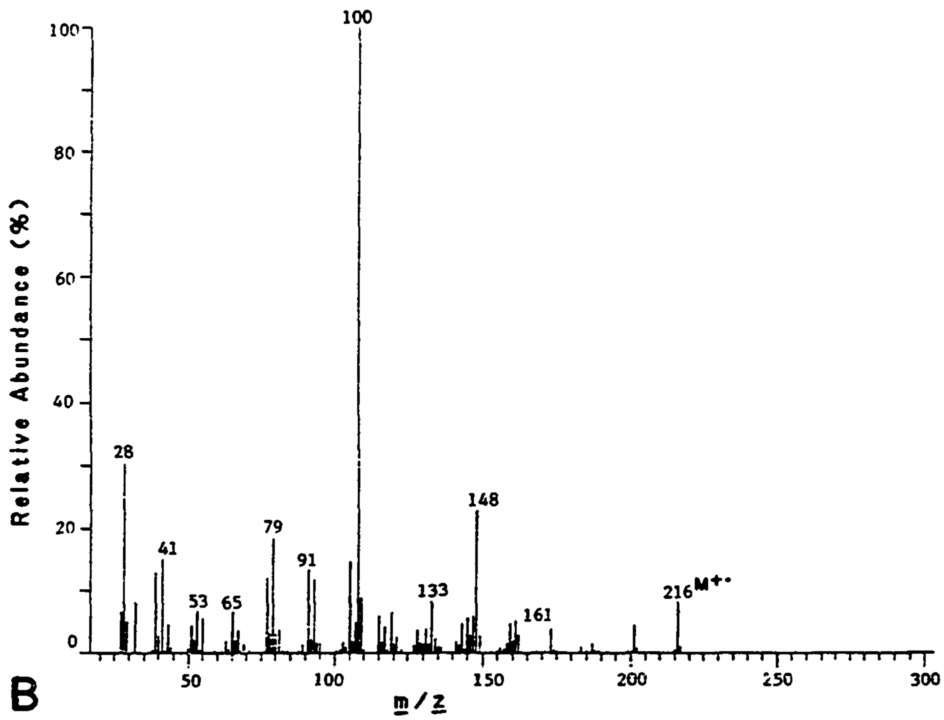

Recorder response
0
Time, minutes
2.91 acetaldehyde
3.02 ethanol
3.27 methylene chloride
3.40 acetic acid
3.68 ethyl acetate
5.01 1,1-diethoxyethane
7.77 3-hexen-1-ol
8.19 1-hexanol
20.50 ocimene quintoxide
22.74 an ethyl methyl phenol
23.45 2-hexenyl acetate
31.90 safrole
32.66 2-undecanone
36.85 delta elemene
37.76 α-cubebene
39.08 a methyleugenol
39.58 α-copaene
40.34 β-elemene
42.32 β -caryophyllene
44.43 α-caryophyllene
45.21 myristicin or isomer
46.47 curzerene
46.71 myristicin or isomer
48.48 Δ -cadinene
48.51 (iso)elemicin
52.26 curzerenone
58.06 germacrone
63.54

Fig. 1.

Fig. 2. Mass spectrum of (A) Curzerenone and (B) Curzerene.

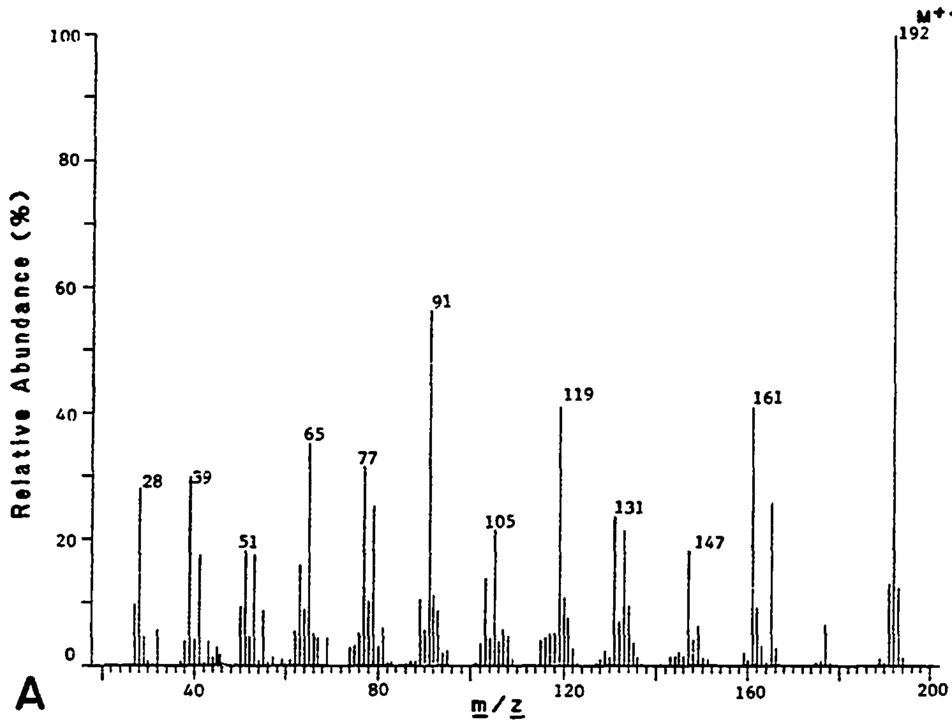

Relative Abundance (%)
0
20
40
60
80
100
28
39
53
66
77
94
105
122
162
187
215
230
M+·
50
100
150
200
250
m/z

A

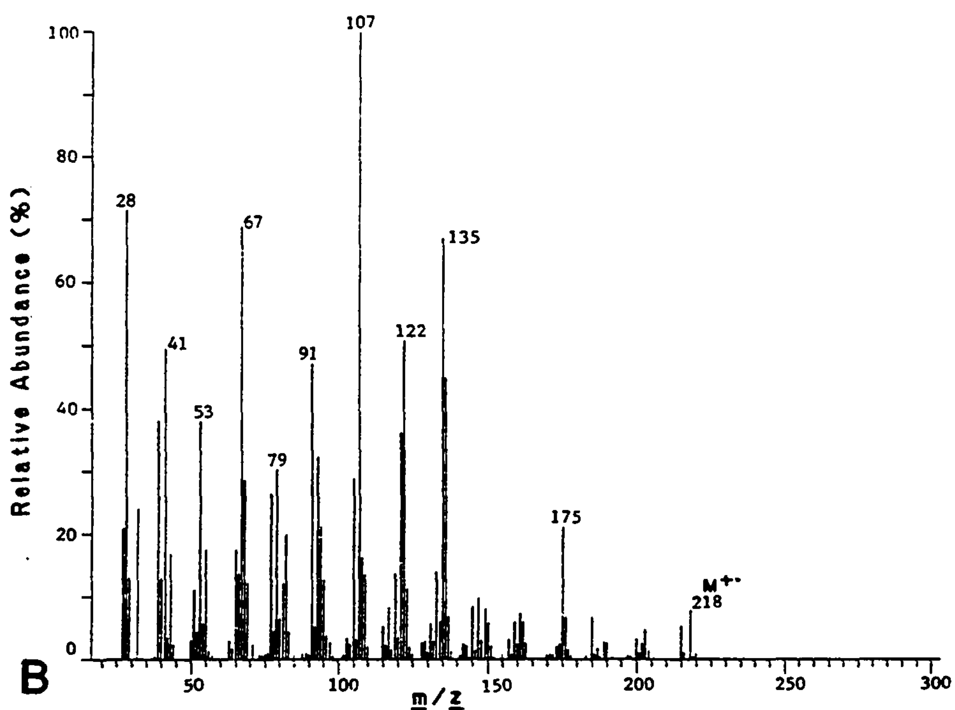

Relative Abundance (%)
0
20
40
60
80
100
28
41
53
65
79
91
100
133
148
161
216
M+·
50
100
150
200
250
300
m/z

B

Fig. 3. Mass spectrum of (A) Myristicin and (B) Germacrone.

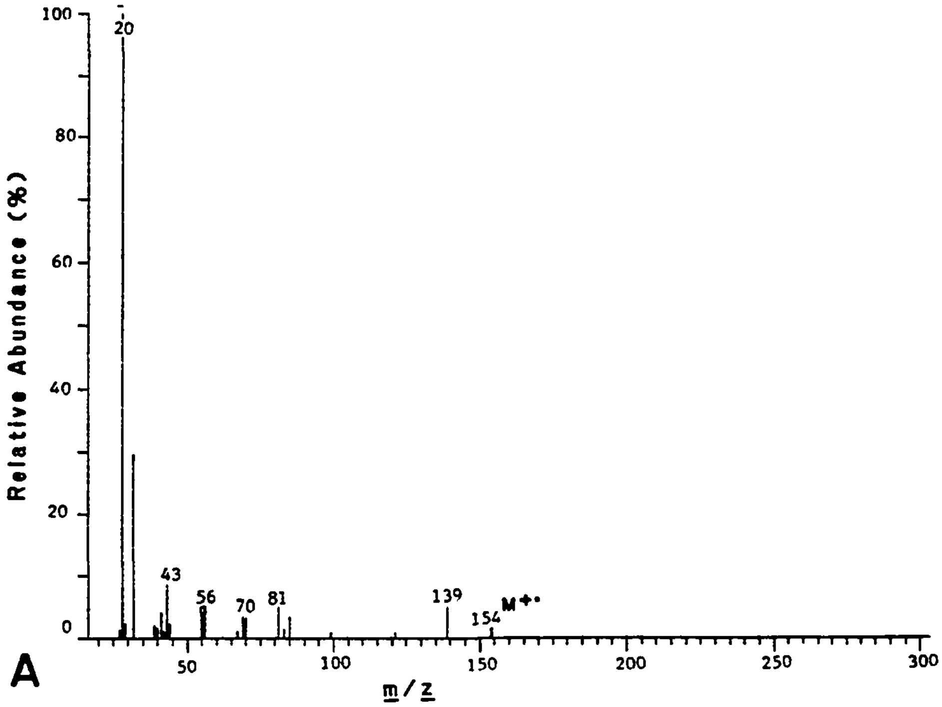

Relative Abundance (%)
m/z
28
39
51
65
77
91
105
119
131
147
161
M+·
192

A


Relative Abundance (%)
m/z
28
41
53
67
79
91
107
122
135
175
M+·
218

B

Fig. 4. Mass spectrum of (A) Ocimene quintoxide.


100
80
60
40
20
0
Relative Abundance (%)
20
43
56
70
81
139
154
M+·
50
100
150
200
250
300
m/z

A

Table 1. Compounds identified in the essential oil from the leaves of *Siparuna guianensis*.

Retention time minutes	Compound[a]	Area percent
2.91	acetaldehyde	0.27
3.02	ethanol	0.51
3.19	ethyl formate	0.27
3.27	methylene chloride	-
3.40	acetic acid	0.48
3.68	ethyl acetate	0.69
5.01	1,1-diethoxyethane	0.13
7.77	3-hexen-1-ol	0.73
8.19	1-hexanol	0.08
20.50	ocimene quintoxide[b]	0.11
22.74	an ethyl methyl phenol (T)	0.03
23.45	2-hexenyl acetate	0.10
31.90	safrole	0.13
32.66	2-undecanone	0.56
36.85	Δ-elemene (T)	0.09
37.76	α-cubebene	0.18
39.08	a methyleugenol	2.86
39.58	α-copaene	0.76
40.09	bourbonene	0.35
40.34	β-elemene (T)	0.63

TABLE 1. Cont.-

42.32	β-caryophyllene	0.84
42.89	a sesquiterpene	0.11
43.31	bergamotene	0.15
43.46	a sesquiterpene	0.16
44.43	α-caryophyllene	0.15
45.21	myristicin or isomer	5.69
46.47	curzerene	0.36
46.71	myristicin or isomer	2.34
47.59	a sesquiterpene	0.15
47.99	a sesquiterpene	0.38
48.48	Δ-cadinene	0.20
48.51	(iso) elemicin	0.25
52.26	curzerenone	25.64
58.06	germacrone	0.76
52.54-63.54	curzerenone types and/or tailing and decomposition to curzerenone	42.31
		88.45

[a]T = tentative.

[b]2,2-dimethyl-5-(1-methyl-1-propenyl)tetrahydrofuran