

The “tortoise’s cajá”—a new species of *Spondias* (Anacardiaceae) from southwestern Amazonia

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Mitchell, J. D. & D. C. Daly (The New York Botanical Garden, Bronx, NY 10458-5127, U.S.A.). The “tortoise’s cajá”—a new species of *Spondias* (Anacardiaceae) from southwestern Amazonia. *Brittonia* 50: 447–451. 1998.—Botanical exploration in southwestern Amazonia has revealed a new species, *Spondias testudinis* J. D. Mitch. & Daly, described and illustrated here. Its distribution appears to be restricted to the Brazilian state of Acre; Pando in Bolivia; and Huánuco and Ucayali in Peru. The sexuality of the flowers of *Spondias* and its implications regarding their morphology is discussed. A provisional key to the neotropical species is presented.

Key words: Amazonia, Anacardiaceae, Neotropics, *Spondias*, taxonomy.

Introduction

As circumscribed here, the genus *Spondias* is represented in the Neotropics by nine species, one of which is a widely cultivated introduction from Oceania, namely *S. dulcis* Parkinson. Sympatric species clusters occur in three distinct regions. In Central America, *S. mombin* L. and *S. radlkoferi* Donn. Sm. are sometimes found in the same locality. In the Atlantic coastal forests of Brazil, *S. mombin*, *S. macrocarpa* Engl., and *S. venulosa* Mart. ex Engl. have all been collected in the same areas, although it is unclear whether these congeners occur in close proximity to one another.

The most recalcitrant taxonomic problems in the genus are found in western and southwestern Amazonia, where at least three native species occur and a fourth is cultivated. One is a rather distinct new species whose common name in Acre, Brazil, is *cajá de jaboti* (“tortoise’s cajá”). Also occurring there is a complex involving the widespread *S. mombin* plus a morphological entity that ranges from eastern Ecuador to northern Bolivia, but the distinctions between these two are blurred by numerous intermediates apparently of hybrid origin. A third entity that probably represents a new taxon is known in Acre by the vernacular

name *cajá-açu* (“big cajá,” in Tupi); it is known thus far only from two fruiting collections from a single locality, and it may be a hybrid between *S. testudinis* (described below) and *S. mombin*.

Molecular and isozyme studies now being carried out by Annemarie Costello at New York University should help us understand the relationships and genetic distances in the *S. mombin* complex. We will publish our revision of neotropical *Spondias* once these studies are completed. In the meantime, the provisional key presented below reflects the current degree of our understanding of the genus.

Sexuality of the Flowers

The scant literature on the floral biology of *Spondias* reports that it is polygamo-dioecious or monoecious and strongly self-incompatible (Bawa, 1974; Bawa & Opler, 1975), but our examination of hundreds of specimens has led us to the conclusion that, with the exception of *S. purpurea* L., the flowers of the neotropical species are structurally and functionally hermaphroditic but strongly protandrous. The evidence can often be found on a single inflorescence. At the time the pollen is shed, the ovary is not developed and the pistil is apparently rep-

resented only by four or five basally fused styles. By the time ovary development is apparent, the dehisced anthers are quite empty and noticeably withered. The point at which the stigmas are receptive is not evident from examination of herbarium material.

Spondias testudinis J. D. Mitchell & Daly, sp. nov. (Fig. 1)

TYPE: BRAZIL. Acre: Mun. Cruzeiro do Sul, Rio Juruá, left bank, Igarapé Viseu, 15 min. upstream by canoe, ca. 8°18'S, 72°44'W, 21 Mar 1992 (fr), *D. C. Daly, L. Ferreira, J. Ramos, L. Lima & F. Walthier* 7559. (HOLOTYPE: HPZ; ISOTYPES: AAU, INPA, L, MG, MO, NY, RB, US).

Foliolis adaxialiter pubescentibus fructuque lenticellato *S. macrocarpa* similis, his notulis autem diversa: foliola lateralia (ob)lanceolata vel elliptica (nec falcato-lanceolata) (2.9–)5.2–7.6 × 1.5–2.3 (nec 5–5.6 × 1–1.4) cm, margo crenulata vel subintegra (vs. crenata), nervi secundarii 15–17 (nec 10–15); pedicellus 1.5–1.7 (nec 2.8–3.5) mm; petala 2–2.4 (nec ca. 2.6) mm; fructus (3.8–)4.9–6.3 × 2.3–2.7 (vs. 3.8–4 × 2.1–2.3) cm.

Tree to 38 m × 65 cm. Outer bark grayish brown with vertical stripes of raised lenticels; inner bark red- and white-striate. *Trichomes* of two types: white, flexuous to crispate suberect hairs to 0.3(–0.4) mm long (on leaves); yellow, appressed to suberect, blunt hairs to 0.2 mm long (on inflorescences). *Leaves* (5–)7–13-jugate, 20–33 cm long; leaflets (sub)opposite; petiole 3.1–5.6 cm long, petiole and rachis densely pubescent; lateral petiolules 1–2 mm, terminal one 0.7–1.7 cm; basal leaflets obliquely ovate to broadly elliptic, 2.9–3.8 × 1.5–2 cm, other laterals obliquely elliptic to (ob)lanceolate, 5.2–7.6 × 1.6–2.3 cm; terminal leaflet symmetric but otherwise like laterals, 5.5–5.9 × 1.4–1.8 cm; leaflet apex acuminate, acumen 0.4–1.3 cm; base oblique, truncate to obtuse; margin crenulate to subentire; on abaxial surface the midrib and secondary veins densely pubescent, hairs scattered to sparse along higher-order veins, on adaxial surface the midrib densely pubescent, rest of surface with scattered hairs, glands scattered on both sides of lamina; midrib prominent abaxially, prominent adaxially, secondary veins in

15–17 pairs, prominulous abaxially, flat adaxially. *Inflorescence* ca. 10–15 cm long; peduncle ca. 1 cm long; axes with scattered to sparse hairs; bracts subtending secondary and higher-order axes lanceolate to narrowly ovate, ca. 1 mm long, sparsely pubescent; pedicel 1.5–1.7 mm long, articulation 0.25–0.4 mm from base, with scattered hairs. *Flowers* calyx lobes deltate, 0.6 mm long; petals narrowly ovate to elliptic, ca. 2–2.4 × 1 mm; perianth glabrous or with a few scattered hairs; antesepalous stamens 3 mm, antepetalous ones 1.5–2.7 mm, anthers 0.7 mm; disk 0.8 mm high; pistil on recently opened flowers 1.5–1.6 mm overall, styles 0.7–0.8 mm long. *Fruits* maturing yellow to orange-brown, essentially oblong, (3.8–)4.9–6.3 × 2.3–2.7 cm (dry), with prominent lenticels. *Seedlings* (based on *Daly et al.* 7251): cotyledons linear, 3.6 cm long; eophylls imparipinnate, 2–3-jugate, leaflets of eophylls lanceolate, laciniately serrate.

Additional specimens examined. BRAZIL. Acre: Reserva Extrativista Chico Mendes, rd. to Seringal Porongaba, Colocação Santo Antônio, 30 km from Brasília, 25 May 1991 (fr), *Cid Ferreira et al.* 10116A (AAU, HPZ, INPA, L, MG, MO, NY, RB); Mun. Cruzeiro do Sul, left bank of Rio Juruá, Igarapé Viseu, ca. 8°18'S, 72°44'W, 21 Mar 1992 (young fr), *Cid Ferreira et al.* 10879 (AAU, HPZ, INPA, L, MG, MO, NY, RB, US); Mun. Brasília, Seringal Piauí, 18 Feb 1984 (fr), *Coelho et al.* 2017 (RB); Mun. Xapuri, Rio Acre, 3 hrs downstream by boat from Xapuri, then 1 hr walking inland from left bank, 10°45'S, 68°28'W, 9 Nov 1991 (st branches + seedling), *Daly et al.* 7251 (AAU, HPZ, INPA, L, MG, MO, NY, RB, US); Mun. Sena Madureira, basin of Rio Purus, Rio Macaua, below Colônia Barro Alto, 9°12.48'S, 68°44.17'W, 4 Apr 1994 (fr), *Daly et al.* 8182 (INPA, NY); Rio Macauã, Colocação Cala Boca, 9°48'S, 69°11'W, 29 Mar 1994 (fr), *L. Lima et al.* 502 (HPZ, NY); Mun. Cruzeiro do Sul, sub-base of Projeto RADAMBRASIL, 23 Feb 1976 (st), *Monteiro & Damiao* 608 (INPA 56.458) (INPA); Mun. Marechal Taumaturgo, Alto Rio Juruá, Reserva Extrativista do Alto Juruá, Colocação Ceará, 9°12'S, 72°44'W, 5 Apr 1993 (fr), *M. Silveira et al.* 475 (CAS, CTES, HPZ, INPA, MEXU, NY, RB); Mun. Sena Madureira, basin of Rio Purus, Fazenda Nova Olinda, Carreador dos Palmares, ca. 8 km from seat of fazenda, 10°07'S, 69°13'W, 21 Oct 1993 (young fr), *M. Silveira et al.* 581 (NY, HPZ).

PERU. **Huanuco:** Prov. Leóncio Prado, Distrito Luyando, pueblo Bolainas B. Sipa, 780 m, 17 Sep 1963 (fl, fr), *A. Gutiérrez R.* 129 (NY); Prov. Puerto Inca, Distrito Yuyapichis, Unidad Modelo de Manejo y Producción Forestal Dantas, 9°40'S, 75°02'W, 1–15 Oct 1990 (fl), *Tello* 354, 396 (NY). **Ucayali:** Prov.

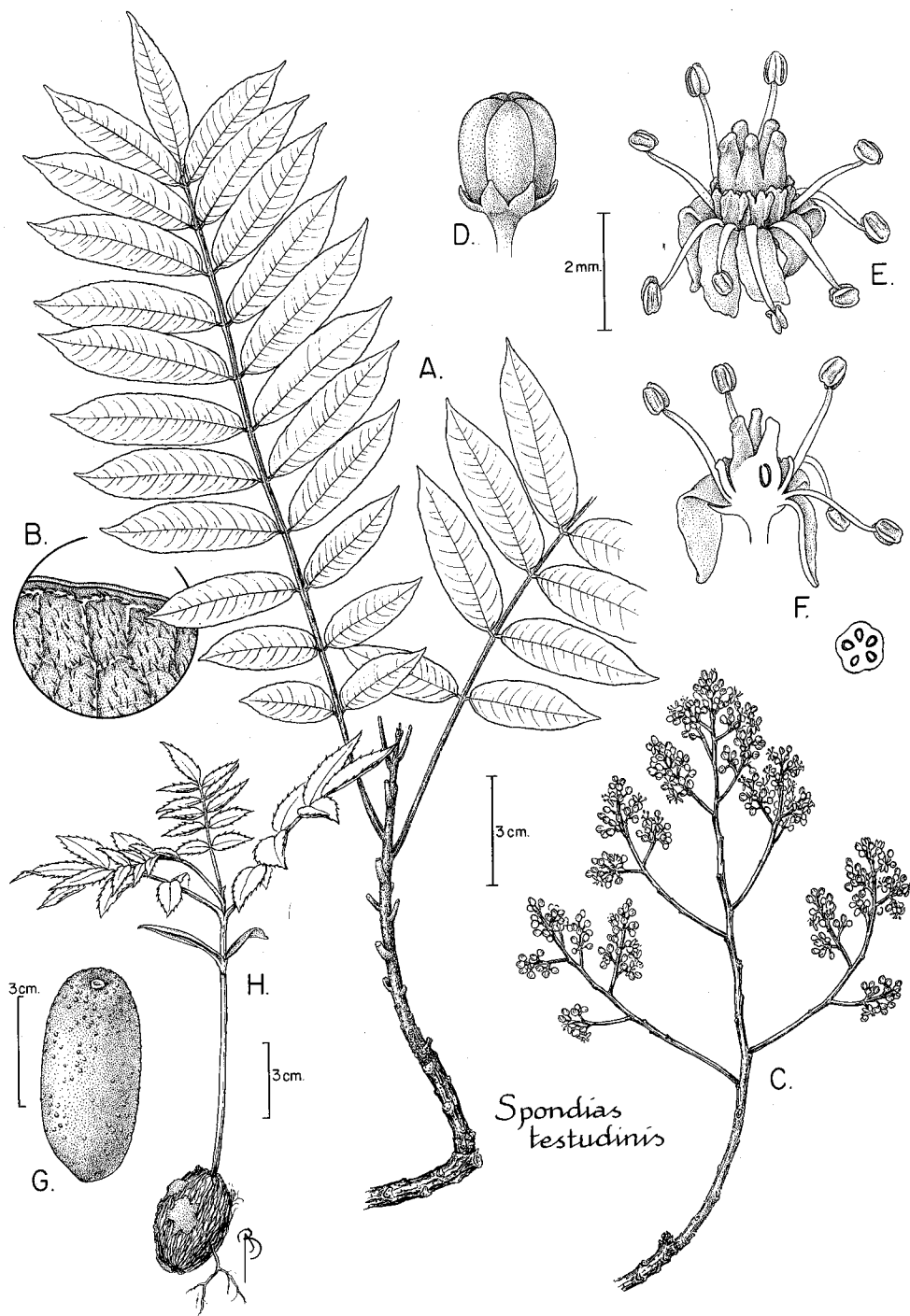


FIG. 1. *Spondias testudinis*. A. Leafy branchlet. B. Detail of abaxial leaflet surface, showing indumentum. C. Inflorescence. D. Flower bud. E. Flower, with anthers dehiscent and ovary developing. F. Longitudinal section of flower, and (detail) transverse section of ovary. G. Mature fruit with lenticellate surface. H. Seedling. (A, B from *R. Lao Magin* 112; C-F from *R. Lao Magin* 83; G from specimen and photo of *Daly* 7559; H from specimen and photo of *Daly* 7251).

2. Leaflet base essentially symmetric, leaflets always glabrous; stone continuous with pedicel, endocarp lacking a fibrous matrix, provided with spiny projections; widely cultivated introduction from Oceania. *S. dulcis* Parkinson
2. Leaflet base asymmetric (sometimes subequal in *S. tuberosa*), leaflets usually with at least scattered trichomes on the petiolules, basal part of leaflet margin, or basal part of abaxial surface; stone free from pedicel at maturity, endocarp with a fibrous matrix, lacking spiny projections; neotropical species but some widely cultivated.
3. Shrubby trees with tortuous branching; roots tuberous; leaves 1-3(-4)-jugate; midrib of leaflet flat to prominulous abaxially; fruit subglobose to obovoid, endocarp compressed; caatinga vegetation of NE Brazil. *S. tuberosa* Arruda
3. Trees without tortuous branching; roots not tuberous; leaves 3-14-jugate, midrib of leaflet prominent (sometimes prominulous in *S. radlkoferi*); fruit oblong, ellipsoid, slightly ovoid, or distinctly obovoid (if obovoid, the apex abruptly short-acuminate when dry); endocarp not compressed; N Mexico to Paraguay and E Brazil.
4. Secondary veins usually distinctly arcuate; fruit maturing green (rarely orange), obovoid, abruptly short-acuminate (dry); tropical dry and moist forests, S Mexico and Central America to NW Venezuela and W Ecuador. *S. radlkoferi* Donn. Sm.
4. Secondary veins essentially straight to very slightly arcuate; fruit maturing yellow or orange(-brown), oblong to ellipsoid to globose, apex rounded to truncate; S Mexico to Paraguay and E Brazil.
5. Leaves (5-)-7-13-jugate, adaxial leaflet lamina sparsely or more often densely pubescent; fruit surface sometimes lenticellate.
6. Lateral leaflets falcate to lanceolate, 5-5.6 × 1-1.4 cm, margin crenate, secondary veins 10-15 pairs; pedicel 2.8-3.5 mm; petals ca. 2.6 mm; fruits 3.8-4 × 2.1-2.3 cm; moist forests of E Brazil. *S. macrocarpa* Engl.
6. Lateral leaflets obliquely elliptic to obliquely (ob)lanceolate, (2.9-)-5.2-7.6 × 1.5-2.3 cm, margin crenulate to subentire, secondary veins 15-17 pairs; pedicel 1.5-1.7 mm; petals 2-2.4 mm; fruits (3.8-)-4.9-6.3 × 2.3-2.7 cm; SW Amazonia. *S. testudinis* J. D. Mitch. & Daly
5. Leaves 3-7-jugate, adaxial leaflet lamina glabrous (sometimes with trichomes on midrib and secondary veins); fruit surface smooth.
7. Bark shed acropetally in long rectangular plates; trichomes crispate, to 0.6 mm long; lateral petiolules 3-10 mm; leaflet margin at base revolute and provided with tufts of long, flexuous trichomes to 0.6 mm; inflorescence axis glabrous, initiated when leaves are incompletely expanded; pedicel 1.6-2(-2.8) mm; petals 1.8-1.9 mm, stamens 1.4-1.5 mm (antepetalous) and 1-1.1 mm (antepetalous), anthers 0.4 mm; moist forests of E Brazil. *S. venulosa* Mart. ex Engl.
7. Bark not shed in long rectangular plates; trichomes straight to arching, to 0.2(-0.3) mm; lateral petiolules 0-3 mm; leaflet margin at base neither revolute nor provided with tufts of trichomes; inflorescence axis variously pubescent, initiated when leaves are completely expanded; pedicel 2-4.5 mm; petals 2.5-3.2 mm, stamens 2.5-2.7 mm (antepetalous) and 2-2.3 mm (antepetalous), anthers 1 mm; native to S Mexico south to Paraguay & E Brazil, widely cultivated in the moist tropics. *S. mombin* L. complex

Acknowledgments

We thank Rupert Barneby for improvements in the Latin diagnosis, Bobbi Angell for the revealing illustration, and the personnel of the HPZ herbarium in Rio Branco, Acre, Brazil. The junior author's field work was supported by National Science Foundation grant no. DEB-9300787 and by the Exxon Foundation; the illustration was paid for by the Fund for Neotropical Plant

Research of The New York Botanical Garden.

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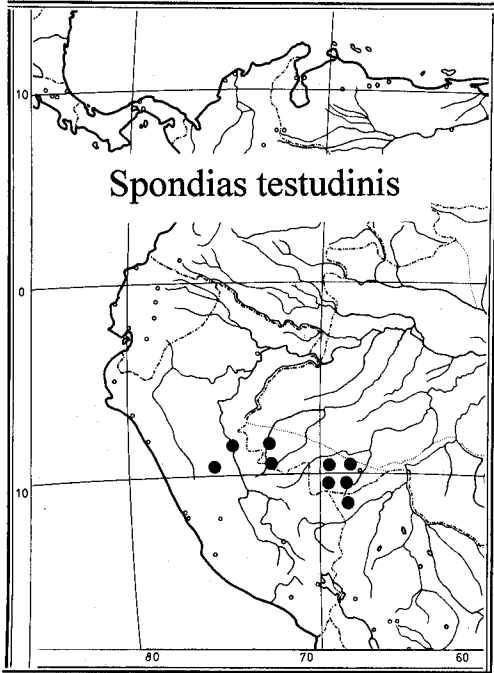


FIG. 2. Distribution of *Spondias testudinis* in southwestern Amazonia.

Coronel Portillo, Distrito Callería, km 4 Pucallpa-Huánuco road, 20 Sep 1963 (fl), *R. Lao Magín* 83 (NY), 2 Dec 1963 (young fr), *R. Lao Magín* 112 (NY); Yarina Cocha, Nueva Esperanza de Panaiillo, 8°15'S, 74°40'W, 148 m, 1 April 1988 (fr), *R. Vásquez & N. Jaramillo* 10481 (NY).

BOLIVIA. Pando: Candelaria, km 36 Cobija-extremo Pando, 15 Jun 1978 (fr), *Brig. Meneces* 690 (INPA).

Distribution and ecology.—The new species is endemic to southwestern Amazonia in Acre, Brazil, and nearby portions of Bolivia (Pando) and Peru (Huánuco, Ucayali) (Fig. 2). It occurs as a canopy or emergent tree in dry to moist tropical forest on terra firme, at 200–780 m. Based on the few col-

lections available, this species is known to flower in September to October and to fruit in September to June.

Common names and uses.—**Brazil:** Acre: *cajá de jaboti*, *cajarana* (“wild cajá”), *cajarana da mata* (“wild cajá of the forest”). **Peru:** Huánuco: *ubos*; Loreto: *ubos colorado* (“red ubos”); Ucayali: *ushum*. **Bolivia.** Pando: *casharana del monte*. Fruit mesocarp edible.

Etymology.—The specific epithet refers to a common name for this species in Acre, Brazil, which means “*Spondias* of the tortoise.”

The new species most closely resembles *S. macrocarpa*, from which the former is distinguished by the following characteristics: lateral leaflets obliquely lanceolate to elliptic (not falcately lanceolate), (2.9–)5.2–7.6 × 1.5–2.3 cm (vs. 5–5.6 × 1–1.4 cm), the margin crenulate to subentire (vs. crenate), secondary veins 15–17 (vs. 10–15); pedicel 1.5–1.7 mm (vs. 2.8–3.5 mm); petals 2–2.4 mm (vs. ca. 2.6 mm); and fruits (3.8–)4.9–6.3 × 2.3–2.7 cm (vs. 3.8–4 × 2.1–2.3 cm).

It differs from the sympatric *S. mombin* in a number of features, including the following: trichomes on leaves flexuous or crispate (vs. always straight), to 0.3(–0.4) mm (vs. to 0.2 mm); leaves (5–)7–13-jugate (vs. 3–7-jugate), the adaxial leaflet lamina sparsely or more often densely pubescent (vs. glabrous or sometimes with trichomes on midrib and secondary veins); fruit surface lenticellate (vs. smooth); eophylls on seedlings imparipinnate, 2–3-jugate (vs. trifoliate) and the eophyll leaflets lanceolate (vs. ovate) and laciniately (vs. simply acutely) serrate (*S. mombin* seedlings described and illustrated in Vogel, 1980).

Key to the neotropical species of *Spondias*

1. Leaflet apex usually obtuse to retuse, occasionally acute; flowering before leaf flush; inflorescence a pseudoracemose, little-branched panicle; flowers only slightly protandrous; sepals rotund to ovate, imbricate in bud; petals red to purple (yellow in one cultivar); stigmas capitate as ovary develops; fruit maturing red to purple (yellow in one cultivar); native to tropical dry forests from N Mexico to SW Ecuador, also widely cultivated and adventive in the tropics. *S. purpurea* L.
1. Leaflet apex acute to acuminate, rarely obtuse (some individuals of *S. radlkoferi*); flowering with or after leaf flush; inflorescence a much-branched panicle; flowers strongly protandrous; sepals deltoid, less often triangular or ovate, separate in bud; petals white to cream to greenish yellow; stigmas oblique as ovary develops; fruit maturing yellow to orange(-brown) to green; N Mexico to Paraguay.