A RECONSIDERATION OF SPONDIAS MOMBIN L.
(ANACARDIACEAE)

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ABSTRACT

Spondias radlkoferi J. Donn. Sm. is considered distinct from Spondias mombin L. It differs chiefly in flowering precociously about one month later than S. mombin, in having fewer styles and a fruit which is green at maturity with an oblong endocarp, in having a trunk with a smooth periderm, and in forming droplets of viscid, cloudy sap when slashed. It is most easily recognized by the villous pubescence of its parts.

The genus Spondias as treated by Blackwell (1967: 363–367) in the Flora of Panama consists of two species, S. purpurea L. and S. mombin L. Field work done on Barro Colorado Island indicates that another taxon, S. radlkoferi J. Donn. Sm., must be segregated from S. mombin L.

The occurrence of the segregate taxon was first brought to my attention by Dr. Dennis Knight (University of Wyoming). After he sampled a number of Spondias by slashing the trunks, he concluded that two taxa were involved since part of the trees sampled produced small droplets of viscid, cloudy sap shortly after having been slashed, while others did not. He believed the plants to be otherwise quite similar. Robin Foster (Duke University), in the course of his phenological studies on Barro Colorado Island, noted other features which separate Spondias into two species. He noted that one group of trees flowers about one month later than do others and that the latter group develop fruits which are elongate and green at maturity. The other Spondias trees produce fruits which are more globose and turn yellow, then orange at maturity.

It was not surprising to discover that at least some native Panamanians were already familiar with part of these differences and had called the green-fruited Spondias “jobo verde.” Mr. James Zetek wrote, in a recently discovered letter at the Field Museum, to Paul Standley on May 6, 1936 from Barro Colorado Island: “Here we have a mombin that resembles the yellow mombin, but it never gets yellow, it stays green all the time.” He also added, “The trunk of the green one is smooth compared to that of the yellow.”

Recent studies have confirmed the observations of Zetek, Knight, and Foster. Other characters have also been found which further delimit Spondias mombin L. and S. radlkoferi J. Donn. Sm.

Spondias radlkoferi is readily distinguished from S. mombin both in the field and in the herbarium. The former usually flowers about a month later than S. mombin, though sufficient overlap occurs in their flowering periods to allow hybridization. Plants of both species may be common in mixed populations on Barro Colorado Islands. However, while they are without question

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closely related species, there is no strong evidence of hybridization. Characters
used to separate the two species are numerous and consistent.

One of the most striking differences between the two species is the precocious
flowering of *Spondias radlkoferi*. Although *S. mombin* flowers, on average,
about one month earlier than *S. radlkoferi*, it generally has fully developed
leaves at time of flowering. *Spondias radlkoferi* begins to flower at about the
time new leaves are developing.

No doubt as a consequence of its later flowering, fruits of *Spondias radlkoferi*
mature later. Moreover they are somewhat larger. The appearance of their
fruit later in the rainy season when food has become slightly more scarce
perhaps explains their lack of an attractive color. Whereas *S. mombin* turns
orange at maturity and is sweet and tasty, *S. radlkoferi* fruits remain green at
maturity and, although edible, they are not sweet and tasty. Their peak of
fruited activity (October-November) comes at a time when competition for
food is greatest, so the species has perhaps lost its ability to produce colored
fruits or never developed it in the first place. Because of the 3-stylar condition
of its flowers, in contrast to the 5-stylar condition of *S. mombin* (discussed
later), it is suggested that *S. radlkoferi* has been derived from *S. mombin* and
probably has lost its ability to produce colored fruits because the serious com-
petition for food in the late dry season has made attractive fruits unnecessary.

On Barro Colorado Island, larger trees produce the bulk of all animal food.
Phenological studies made in central Panama (Croat, 1969) indicate that the
peak of the fruiting season for medium- to large-sized trees occurs in April and
then tapers off until a low is reached in November when fruit is always very
scarce. Since the peak of fruiting for *Spondias radlkoferi* usually occurs during
October and November when fruit is most scarce, the species has no difficulty
getting an abundance of animals to disperse even its unattractive, not-so-tasty
fruits. The fact that it is apparently as abundant as *S. mombin*, which has
attractive, tasty fruits, attests to this.

There are several other good field characters which may be used to separate
the two closely related species. The appearance of the bark of the trunk and
larger branches offers one of the most characteristic features. While there is
some variability from tree to tree, *Spondias radlkoferi* has a trunk with a relatively
smooth surface with paper-thin strips of grayish periderm oriented vertically
(Fig. 1). The intervening brownish areas are roughened but not raised. In
*S. mombin*, the thin grayish strips of periderm are missing and are replaced by
much thicker, coarse sections of periderm 1–2 cm wide which are considerably
raised from the intervening areas of the trunk (Fig. 2). These thick, irregular
patches may contain further elevated, somewhat rounded projections to 7–8
mm high. The intervening area of the trunk is flat but variously fissured in an
irregular vertical pattern. Occasionally the lowermost part of the trunk may
lack the raised warty strips of periderm. Instead this area usually has a more
or less continuous pattern of broad, shallow depressions.

The inner bark of both species is similar. Though quite variable from
tree to tree, the inner bark is pink to reddish with whitish, narrowly wedge-shaped
areas protruding inward from the periphery (Fig. 3). The surface of the inner
bark of Spondias radlkoferi forms minute, whitish, viscid droplets, easily visible within 30-60 seconds after slashing. Generally the droplets do not increase greatly in size nor do they coalesce or form a stream of sap. However, felled trees may form abundant, runny sap (Fig. 3). In contrast, S. mombin shows no evidence of whitish, viscid sap and does not form the small droplets on the inner bark after it has been slashed.

Another distinguishing field character is the appearance of the old fruit endocarps, which generally lie in great abundance beneath trees of both species for most of the year. While some animals, particularly rodents such as the agouti (Dasyprocta punctata) and other frugivores, carry many of the fruits away and bury them (Smythe, 1970), monkeys eat the fruit covering in the tree, dropping the inedible endocarp directly to the ground. These weathered endocarps alone are adequate for determination of the tree. The endocarps of Spondias mombin are obovoid, 2-2.5 cm long, whereas those of S. radlkoferi are oblong, usually 3 cm or more long (Fig. 4).

Those features distinguishing the two species on herbarium specimens are many and varied. The most easily observed definitive character is that of pubescence, although after a number of specimens are examined the color of a dry specimen is adequate for determination. Specimens of Spondias radlkoferi dry blackened, while those of S. mombin dry greenish. Spondias mombin
Table 1. Field characters separating *Spondias mombin* L. and *S. radlkoferi* J. Donn. Sm.

<table>
<thead>
<tr>
<th><strong>S. mombin</strong></th>
<th><strong>S. radlkoferi</strong></th>
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<tbody>
<tr>
<td>Bark very coarse, deeply fissured the intervening corky periderm hard and prominently raised.</td>
<td>Bark not deeply fissured, the strips of periderm paper-thin, smooth.</td>
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<tr>
<td>Slash not producing cloudy, viscid droplets on inner bark.</td>
<td>Slash producing cloudy, viscid droplets within 30–60 seconds on inner bark.</td>
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<tr>
<td>Old endocarps (persisting on ground beneath tree for most of the year) oblong.</td>
<td>Old endocarps oblong.</td>
</tr>
<tr>
<td>Leaves generally fully developed at time of flowering (ca. 1 month earlier than <em>S. radlkoferi</em>).</td>
<td>Leaves usually young at time of flowering.</td>
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<tr>
<td>Mature fruits orange, sweet, and tasty.</td>
<td>Mature fruits green, edible but not very tasty and reported by some to be more acidic.</td>
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is sometimes nearly glabrous, but any pubescence consists of short, puberulent trichomes. The species is reasonably uniform throughout its range in this respect, but the trichomes are longer in Mexico. *Spondias radlkoferi* is sparsely to densely villous, especially on the veins of the lower leaf surface and branches of the inflorescence. Trichomes are crisped or straight and are usually curly or at least recurved near the middle.

Although the inflorescence of *Spondias radlkoferi* occurs precociously or nearly so, its flowers do not differ greatly from those of *S. mombin*. The most easily distinguished difference is the generally glabrous pedicel and calyx. This contrasts sharply with the usually densely pubescent branchlets of the inflorescence. Costa Rican and other Central American specimens often have some pubescence on the pedicel, but the trichomes are sparse and long. The pedicel and calyx of *S. mombin* are usually moderately to densely short-puberulent.

In addition there are characters not so easily observed such as shape of the flower buds (ovoid in *Spondias radlkoferi* vs. round to obvoid in *S. mombin*), length of the calyx lobes (much deeper in *S. radlkoferi*), and thickness of the disk. The disk of *S. radlkoferi* is ca. 2.3 mm wide and broader than the width of the stylar chump, whereas the disk of *S. mombin* is only about 1 mm wide and narrower than the stylar chump.

Finally there are significant differences in the number of styles for the two species. *Spondias mombin* generally has 5 styles, less frequently it may have up to half of the flowers with 4 styles and rarely do flowers have only 3 styles. On the other hand, *S. radlkoferi* generally has flowers with 3 or 4 styles (in actual counts of ca. 50 flowers, 60% were 4-stylar and 40% were 3-stylar), very rarely with 5 styles.

There are strong indications that the 3- and 4-stylar conditions have arisen directly from the 5-stylar condition. Analysis of the number of styles on both flowers and juvenile fruits from the same plants invariably shows more fruits with 5 styles than flowers with 5 styles. Since there is no reason to believe that
a flower with 5 styles is more apt to produce fruit than one with 3 or 4, I believe
the 4-stylar condition in flowers is often the result of fusion of 2 styles. In a
few rare cases the fourth style was seen in the process of pulling apart on a
maturing fruit. This is clear evidence that many of the 4-stylar flowers (and
for the same reason, the 3-stylar flowers) are the result of a fusion of styles.
It is not certain whether fusion of the styles in this manner is detrimental. Both
Spondias mombin and S. radikoferi appear to have 5-locular fruits, and thus
the united styles apparently function as 2 separate styles. The fact remains,
however, that the degree of style fusion is more advanced in S. radikoferi than
in S. mombin.

The characters used in the key were selected because they are usually the
easiest to observe on dried herbarium specimens. They are no more definitive
however than a variety of other characters. Table 1 lists other sets of con-
trasting characters useful in separating the two species in the field.

# Key

Plants glabrous or pubescent parts of plant merely puberulent (the trichomes short and
straight); leaves not drying blackened, usually fully developed at time of flowering;
blades with a prominent submarginal collecting nerve; calyx pubescent

Plants villous to velutinous (the trichomes not straight or if so long and very dense); leaves
usually drying blackened, usually not fully developed at time of flowering; blades
lacking a submarginal nerve; calyx glabrous

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**Spondias mombin** L., Sp. Pl. 371. 1753.—“Hogplum.”


*T. tree* mostly 10–30 m tall, to 60 cm d.b.h.; periderm gray, deeply and
coarsely fissured, the raised segments hard, rough, the inner margin irregular;
near bark variously colored, usually with triangular patches of red or tangerine
alternating with white; at least the youngest branchlets puberulent. *Leaves*
imparipinnate, alternate, to 60 cm long (to 70 cm on juveniles); petiole and
rachis usually finely puberulent; leaflets mostly (3–)9–17, opposite or sub-
opposite; petiolules 6–9(–14) mm long; blades oblong to ovate, usually acuminate,
a cute to rounded and asymmetrical at base, 3–20 cm long and 1.5–7 cm wide,
usually ± glabrous except for puberulence on midribs and major veins above
and below; reticulate nerves prominulous, the margin minutely revolute with
a prominent submarginal nerve; the larger leaflets with the midrib arched.
*Panicles* terminal, to 60 cm long; branches, peduncles, pedicels and calyces
usually puberulent; *flowers* 5–7 mm wide, 5-parted, globular to obovoid in bud;
pedicels 1–5 mm long, usually articulate near the base; calyx shallow, the lobes
short, triangular, sharply acute, usually minutely puberulent, the margins ciliate;
petals white, acute and in flexed-apiculate at apex, somewhat reflexed at anthesis;
stamens 10, exerted, 1.5–3 mm long, alternating with the fleshy, undulate seg-
ments of the disk; disk fleshy, undulate-lobed, to ca. 1 mm wide, the width of
one side less than the width of the clump of styles; styles usually 4 or 5 (rarely
3), much shorter than stamens at anthesis, the stigma linear, on the dorsal surface
near apex. *Fruit* oblong to obovoid, 2.5-3 cm long, yellow to orange at maturity; mesocarp to 6 mm thick, fleshy, sweet and tasty; endocarps obovoid, 2-2.5 cm long, hard, covered by a tough, coarse, fibrous matrix.

Flowering principally from March to June (rarely earlier), but most abundant in April and May. Fruits are mature from July to October, mostly in August and September. Leaves are lost during the early part of the dry season beginning in December and January and are replaced before flowering commences.

Throughout tropical America. Introduced in tropical Africa. In Panama principally from tropical moist forest in the Canal Zone and the Provinces of Bocas del Toro, Colón, Panamá and Darién; also known from premontane moist forest in Panamá Province (Farfan Beach), tropical dry forest in Cocle and premontane wet forest in Chiriquí (Progresso).

Since *S. mombin* and *S. radlkoferi* were lumped in the *Flora of Panama* (Blackwell, 1967: 363-367), the following list of exsiccatea from Panama is published here for clarification.


**Spondias radlkoferi** J. Donn. Sm., Bot. Gaz. (Crawfordsville) 16: 194. 1891.


Tree to 30 m tall, to 75 cm d.b.h.; periderm not deeply fissured, the surface with thin, narrow strips of periderm; inner bark similar to *S. mombin* except producing whitish, viscid droplets within a short time after being cut; younger branches glabrate to sparsely crisp-villous to densely villous, becoming glabrate. *Leaves* imparipinnate, alternate, to 54 cm long, usually sparsely crisp-villous on petiole, rachis, upper midrib and lower surface of leaflets, especially on younger leaves; leaflets mostly 7-19; blades ovate to oblone-elliptic or oblong, abruptly long acuminate, acute to subcordate and markedly inequilateral at base, 2.5-16 cm long and 1.8-6 cm wide, the margins ± revolute, usually ciliate,
usually lacking a submarginal nerve. Flowers 5-parted, usually bisexual, rarely pistillate, the first open flowers usually appearing with the new leaves in terminal and upper axillary panicles to 55 cm long; axes and rarely pedicels sparsely to densely crisp-villous; pedicels glabrous or less often pubescent, articulate usually 0.5–2.5 mm below the calyx (the articulation sometimes obscured by bracteoles); flower buds usually ± pyriform; calyx cupulate, the lobes thick, prominent, rounded to blunt-triangular, ca. 1 mm long, usually glabrous throughout; pedicels ± oblong-elliptic, acute and infl exed-apiculate at apex, 3-nerved (including marginal nerve), 2.3–4.3 mm long, white or greenish-white, recurved at anthesis; stamens 10, 1.7–2 mm long, in 2 series, exerted at anthesis; disk to 2.3 mm wide, fleshy, undulate-lobed, the width of one side more than the width of the clump of styles; ovary subglobose, pubescent; styles usually 3 or 4 (rarely 5), usually free and shorter than the stamens at anthesis in bisexual flowers, the stigmatic surfaces linear, on the dorsal surface near the apex: female flowers rare, the styles to ca. 2 mm long, ca. twice as long as the stamens, united below the middle, the stigmatic surface ovate, turned inward. Fruit 3–3.5 cm long, minutely pubescent when immature, oblong to obovate and green at maturity; mesocarp thin, green with a ± unripened flavor, faintly sweet to acidic; endocarp oblong, nearly as long as fruit, hard, covered by a tough, coarse, fibrous matrix.

Plants often flower 4–6 weeks later than S. mombin on Barro Colorado Island, but since their flowering periods overlap, they may be seen flowering together. Flowers occur mostly April to July, especially May and June. Fruits mature from September to December, especially October and November.

Southern Mexico (Veracruz, Chiapas, Campeche), throughout Central America, into Colombia and Venezuela. In Panama known principally from tropical moist forest in the Canal Zone and Panamá Province (El Llano) but also known from tropical moist forest in Bocas del Toro and from premontane wet forest in Chiriquí (Finca Linda to Boquete).

**MEXICO.** Campeche: Tuxpena, Lundell 894 (f, mo). Chiapas: Escuintla, Calaculata, Matuda 16668 (f), Veracruz: Fortunio, Coatacoalcos River, Llewellyn Williams 8694 (mo). Yucatán: Gaumer 24069, 24070 (both f); Southeast Kancabonot, Gaumer 23885 (f).

**Guatemala.** Alta Verapaz: Near Alta Verapaz-Petén border, Steyermark 45214 (f). Chiriquimula: Caracol Mts. 1.5 mi. N of Quezaltepeque, Steyermark 31408 (f), IZÁBAL: Valley of Río Motaqua, Steyermark 39348 (f). PETEN: Camino Melchor K 32, 250 m, Aguilar 37 (f). Quetzaltenango: Between Colombia and Coatepeque, 850 m, Steyermark 52128 (f). BETAHULEU: Region of Ajasa E of Santa Cruz Mulua, 330 m, Standley 88210 (f).

**San Marcos:** Volcán Tajumulco, 1300–1500 m, Steyermark 37141 (f). PROVINCE UNKNOWN: Río Dulce, Wilson 409 (f).

**BELIZE.** Corozal-San Antonio Road, Gentle 130 (f), Lundell 424 (f), 5017 (f, mo), Wm. C. Meyer 190 (f). Honey Camp, Orange Walk, Lundell 116 (f).


**NICARAGUA.** Region of Braggman’s Bluff, Englesing 223 (f).

**EL SALVADOR.** Allen & van Severen 6890 (f).


**PANAMA.** Bocas del Toro: Bocas del Toro, Dunlap 504 (mo). CANAL ZONE: Barro
Colorado Island, Acuiles 10 (mo), Croat 4912, 4929, 6040, 6453, 6838, 9046, 9101, 9283, 10082, 10218, 10227, 10294, 10320, 10328, 10836, 11157, 11682, 12580, 14404a (all mo), Dwyer 1458 (mo), Ebinger 392 (f), Foster 861, 1652 (both mo), Knight 69–31 (mo), Shattuck 82 (f, mo), Starry 106 (mo), Zetek 3414, 3584, 3645 (all f, mo), 3854, 4998 (both mo). Gaillard Highway near Gamboa, Croat 14476 (mo). Gaillard Highway near Summit Garden Croat 14830 (mo). Road to Gamboa airport Croat 14841 (mo). Along canal near gate to Pipeline Road, Croat 14837 (mo). Pipeline Road near gate, Croat 16681 (mo). 2 mi. E of El Llano, Tyson 1757 (mo), CHIRIQUI: Finca Lerida to Boquete, ca. 1300–1700 m, Woodson et al. 1109 (mo). PANAMA: Vicinity of El Llano, Duke 5869 (mo).

VENEZUELA. Without exact locality, Birschel s.n. (f).

LITERATURE CITED


