

DOMESTICATION, HYBRIDIZATION, SPECIATION, AND THE ORIGINS OF AN ECONOMICALLY IMPORTANT TREE CROP OF *SPONDIAS* (ANACARDIACEAE) FROM THE BRAZILIAN CAATINGA DRY FOREST

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ABSTRACT

Domestication can be defined as evolution driven by artificial selection by humans, where individuals possessing desirable characteristics are favored and selectively propagated; over time this process leads to morphological, physiological and genetic changes that distinguish domesticated taxa from their wild ancestors, many times to the point in that the domesticated taxon is regarded as a distinct species. In this paper we address plants of *Spondias* known by the vernacular name *umbu-cajá* in Northeast Brazil. These plants are found in managed landscapes, but natural populations have not been identified due to widespread cultivation coupled with the clearing of original vegetation. *Umbu-cajá* can be regarded as domesticated because it appears to occur exclusively in cultivation, being actively maintained and propagated by man due to its juicy, delicious fruits. *Umbu-cajá* is referred to as being of hybrid origin in the literature, but this hypothesis remains largely untested experimentally. We carried out a thorough comparative examination of the overall morphology and also a morphometric analysis of leaf and fruit characters of populations of *umbu-cajá* and other *Spondias* species found in Northeast Brazil. We also reconstructed phylogenies and haplotype networks based on sequences of two non-coding cpDNA regions and the nuclear ETS region in order to ascertain the genetic affinities of *umbu-cajá*. Additionally we estimated the ages of diversification events in *Spondias* in order to determine when *umbu-cajá* diverged from related species. Although displaying some morphometric intermediacy in the leaves, a number of morphological features readily distinguish *umbu-cajá* from its nearest relatives *Spondias tuberosa* and *S. venulosa*. No haplotypes were found to be shared between distinct *Spondias* species, except in the ETS dataset where *umbu-cajá* and *S. tuberosa* shared the same haplotype. In the cpDNA dataset, haplotypes of *umbu-cajá* are nearest to haplotypes of *S. venulosa*, but genetic distances within each taxon are smaller than the genetic distance between the two taxa, suggesting different gene pools for each taxon. There is incongruence in the placement of *umbu-cajá* haplotypes in the cpDNA versus ETS datasets, and also incongruence in the trees recovered from the phylogenetic analyses of both datasets, which is an indication that *umbu-cajá* might have a hybrid origin with *S. venulosa* and *S. tuberosa* as its parents. However, *umbu-cajá* was found to have diverged from *S. venulosa* 3.79 million years ago, indicating that this taxon originated from natural processes. Based on the results of the molecular, morphometric, morphological and time divergence investigations we conclude that *umbu-cajá* should be regarded as distinct lineage that remained undescribed because at present it seems to be only known from cultivation, and also due to its putative hybrid origin. We therefore describe this taxon as *Spondias bahiensis* sp. nov.

Domestication is evolution driven by artificial selection by man: the human use of a species with the favoring of individuals possessing desirable characteristics (Heiser 1988; Zohary 2004). It is a cumulative process that results in changes in the frequency of the species' phenotypes, with higher frequencies of the preferred phenotypes; this process can be either intentional or unintentional ("unconscious": Heiser 1988; Zohary 2004). Over time, the process of domestication results in morphological, physiological and genetic changes that distinguish domesticated taxa from their wild ancestors (Doebley et al. 2006), what has been described as the "domestication syndrome" (Gepts 2004). The genetic and morphological changes that compose the domestication syndrome involve a variety of mechanisms, and are relatively well documented for a number of annual plant crops, but less so for perennial plant crops (Zohary 2004; Miller & Gross 2011; Goldschmidt 2013). The domestication process in perennial plant crops differs from that occurring in annual crops in how these crops are maintained, with vegetative propagation being usual for perennial crops, while sexual reproduction is the norm for annual crops (Zohary 2004; Miller & Gross 2011). Therefore, perennial crops are separated from their wild ancestors by a smaller number of generations than annual crops (Zohary 2004), and many changes associated with domestication that are observed in annual crops do not occur in perennial crops (Miller & Gross 2011). Domesticated perennial crops can thus vary greatly in their degree of domestication, ranging from almost no change from wild forms to cultivated forms markedly different from wild forms, depending on the selection pressures that the species has undergone during the domestication process.

Among the plant families including species domesticated as food sources is Anacardiaceae R.Br., a family of some 800 species distributed in subtropical and tropical zones worldwide

(Pell et al. 2011). Anacardiaceae has many species which are cultivated for their edible fruits or seeds, some ranking as very important food sources, such as mango (*Mangifera indica* L.), cashew (*Anacardium occidentale* L.), pistachio (*Pistacia vera* L.), and pink peppercorn (*Schinus terebinthifolius* Raddi) (Pell et al. 2011). For instance, mango ranks among the five most important fruit crops in the world (Janick 2005). Many other Anacardiaceae are used as food sources on a regional scale, including species in the genera *Antrocaryon* Pierre, *Buchanania* Spreng., *Choerospondias* B.L.Burt & A.W. Hill, *Cyrtocarpa* Kunth, *Harpephyllum* Bernhardt ex Krauss, *Lannea* A. Rich., *Ozoroa* Delile, *Rhus* L., *Searsia* F.A. Barkley, *Sclerocarya* Hochst., *Spondias* L., *Tapirira* Aubl., and *Trichoscypha* Hook. f. (Pell et al. 2011).

Spondias comprises ca. 18 species native to tropical areas of the Americas, Asia, and Madagascar (Mitchell et al. 2012). All *Spondias* species possess edible fruits, and some of the species are highly valued for the very agreeable taste of their fruits; these species are therefore widely cultivated both on a regional scale (e.g. *S. pinnata* (L. f.) Kurz, *S. tuberosa* Arruda) and pantropically (*S. dulcis* Parkinson, *S. mombin* L., *S. purpurea* L.). In spite of the number of species taken to cultivation, there are few studies focusing on the domestication process in *Spondias*. Exceptions are the thorough investigation of the domestication of *S. purpurea* in Mesoamerica (Miller & Schaal 2005; Miller & Schaal 2006; Miller & Knouft 2006; Miller 2008) and the management of wild populations and incipient domestication process of *S. tuberosa* (Lins-Neto et al. 2010; Lins-Neto et al. 2012; Lins-Neto et al. 2013).

Eight *Spondias* species are found in Brazil: three are introduced and cultivated and five are native to the country, of which three are Brazilian endemics (Table 1). Besides the known species, there are plants belonging to *Spondias* in the Northeastern region of Brazil which are known by the

vernacular names *umbu-cajá*, *umbu-cajazeira*, *cajá-umbu* and *cajá-umbuzeiro*. These plants are found in managed landscapes (Carvalho 2006; Ritzinger et al. 2006; Ritzinger et al. 2008a; Soares-Filho 2011), and thus far natural populations have not been identified. It is unclear whether or not natural populations of *umbu-cajá* exist: widespread cultivation coupled with the clearing of original vegetation have obscured the origins of these plants. *Umbu-cajá* can be regarded as domesticated since it appears to occur exclusively in cultivation, being actively maintained and propagated by man (Gepts 2004; Pickersgill 2007; Meyer et al. 2012).

There is evidence of the existence of at least two distinct *umbu-cajá* taxa (Carvalho 2006): a northern *umbu-cajá* taxon whose center of diversity lies within the states of Ceará, Paraíba and Rio Grande do Norte, and a southern *umbu-cajá* taxon whose center of diversity lies within the state of Bahia. The northern *umbu-cajá* is also found in Alagoas, Pernambuco, Piauí, and Sergipe, as the result of introduction and cultivation by man; likewise, the Bahian taxon is also found in northern Minas Gerais, Pernambuco and Sergipe (Figure 1). The two taxa differ considerably in gross morphology, including the dimensions of the plants, leaf size, number and morphology of leaflets, and morphology of inflorescence and fruits. Due to the fact that both taxa possess the same vernacular name, there is much confusion in the literature, with authors investigating one taxon often citing studies where the other taxon has been investigated instead. This study focus on the *umbu-cajá* taxon found the state of Bahia, and henceforth all mentions to the vernacular name *umbu-cajá* refer to Bahian taxon, unless otherwise stated. The same applies to references cited herein for *umbu-cajá*.

Fruits of *umbu-cajá* are valued because they possess a thick, juicy mesocarp similar to that found in fruits of *umbu* (*Spondias tuberosa*) but less acidic and with a distinct aroma and flavor. The relatively low stature

of the plants facilitates the collection of fruits. Plants are found throughout the state of Bahia in informal agricultural habitats such as backyard gardens and small multicrop farms (Carvalho 2006; Ritzinger et al. 2006; Ritzinger et al. 2008b; Santana et al. 2011a; Santana et al. 2011b). *Umbu-cajá* fruits are consumed locally and also marketed both locally and regionally. Fruits are eaten fresh, and also used to make juices, jams and other products (Ritzinger et al. 2006; Carvalho et al. 2008; Romano et al. 2011; Romano et al. 2013). The gathering and sale of *umbu-cajá* fruits represent a considerable source of income for many families at harvest time.

Umbu-cajá fruits are increasingly attracting the attention of the food processing industry for use in the preparation of jam (Carvalho 2010; Mamede et al. 2013), conserve (Ferreira et al. 2009; Fiaes et al. 2009; Ferreira 2010; Fonseca et al. 2010a, 2010b), fruit paste/cheese (Ferreira 2010), and frozen fruit pulp (Carvalho et al. 2008; Santos 2009b; Santos et al. 2013) – the latter is used in the preparation of fruit juice and ice-cream, and is currently the main industrialized product of *umbu-cajá*. However, the bulk of *umbu-cajá* production still derives from backyard gardens. Only recently superior cultivars are being actively selected (Carvalho 2006; Soares-Filho & Ritzinger 2006; Carvalho et al. 2008; Ritzinger et al. 2008b; Santana et al. 2011a; Santana et al. 2011b; Soares-Filho 2011; Lima 2012; Santos et al. 2012) and their large-scale production in orchards being promoted (Romano et al. 2011; Soares-Filho 2011; Romano et al. 2013). Actions are also being taken towards the dissemination of propagules among poor rural communities (Soares-Filho 2011; Fonseca & Oliveira 2012; Romano et al. 2013).

The growing interest in *umbu-cajá* as a crop has encouraged initiatives aimed at characterizing and implementing germplasm collections with the purpose of preserving the existing genetic diversity (Carvalho et al. 2001; Ritzinger et al. 2008; Soares-Filho 2011; Silva-Júnior et al. 2012) and quick methods to select superior cultivars (Santos

Table 1. *Spondias* species found in Brazil.

Species	Distribution
+ <i>Spondias dulcis</i> Parkinson	Originally from Society Islands (Kostermans 1991), Polynesia (Campbell & Sauls 1994), widely cultivated pantropically
+ <i>Spondias pinnata</i> (L.f.) Kurtz	Originally from India to Myanmar and Thailand (Kostermans 1991), sporadically cultivated elsewhere, in Brazil found in a few collections
+ <i>Spondias purpurea</i> L.	Originally from Mexico and Central America (Miller & Schaal 2005), widely cultivated pantropically
* <i>Spondias macrocarpa</i> Engl.	Brazil, found in humid forests in southern Bahia, Espírito Santo, southeastern Minas Gerais and Rio de Janeiro states
<i>Spondias mombin</i> L.	Widely distributed in the neotropics, naturalized in parts of Africa (Duvall 2006), widely cultivated pantropically
<i>Spondias testudinis</i> J.D.Mitch. & Daly	Restricted to a small area in Bolivia (Pando), Brazil (Acre), and Peru (Huanuco, Ucayali) (Mitchell & Daly 1998)
* <i>Spondias tuberosa</i> Arruda	Brazil, found in most states of Northeastern Brazil and in the northern region of Minas Gerais state, growing in the Caatinga seasonally dry woodlands; sporadically cultivated elsewhere
* <i>Spondias venulosa</i> (Engl.) Engl.	Brazil, occurring in semi-deciduous forests in Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro states

Species marked with a plus sign (+) are introduced. Species marked with an asterisk (*) are Brazilian endemics restricted to the Eastern regions of the country.

et al. 2010). Other studies have been carried out focusing on various biological aspects of *umbu-cajá*, such as flowering phenology and fruit set rates in different clones (Cruz et al. 2009; Cruz & Ritzinger 2010; Cruz et al. 2010), optimal methods for the propagation of superior cultivars (Araújo & Oliveira 2009; Santos 2009a; Bastos 2010; Lima 2012) and methods to improve its production in more extreme semiarid conditions through grafting on *Spondias tuberosa* rootstock (Santos et al. 2002; Araújo et al. 2006; Santos & Lima-Filho 2008; Araújo & Oliveira 2009; Lima-Filho & Santos 2009a; Araújo et al. 2010; Aidar et al. 2013).

The current acceptance of *umbu-cajá* has also promoted a wide range of studies aimed at its industrial use, such as the investigation of physical, physical-chemical and chemical features of fruits (Carvalho 2006; Carvalho et al. 2008; Ritzinger et al. 2008; Santos et al. 2008b; Santos 2009b; Santos et al. 2009; Lima et al. 2010; Santana et al. 2010; Santos 2010; Santos et al. 2010; Lima 2012; Santos

et al. 2012), physical, chemical, and microbiological stability of frozen pulp (Santos et al. 2013), color and carotenoid composition of different clones (Gomes et al. 2009), and the characterization and inactivation of degrading enzymes (Silva & Koblitz 2010; Barros et al. 2011; Lima et al. 2011). Leaf extracts of *umbu-cajá* have also been found to possess antimicrobial activity (Silva et al. 2012). *Umbu-cajá* is susceptible to infestation by fruit flies, which may cause devaluation and/or reduction of fruit production due to damage in appearance and quality of the fruits. Because of this a number of studies have been carried out aimed at investigating the identity of the fruit flies (Santos 2003; Santos et al. 2004; Santos et al. 2005; Lima-Júnior et al. 2007; Barbosa et al. 2012; Melo et al. 2012) which attack *umbu-cajá* fruits, and the interactions of fruit flies with native and exotic parasitoid wasps used for their biological control (Bomfim 2007; Lima-Júnior et al. 2007; Santos et al. 2008c; Bomfim et al. 2010;

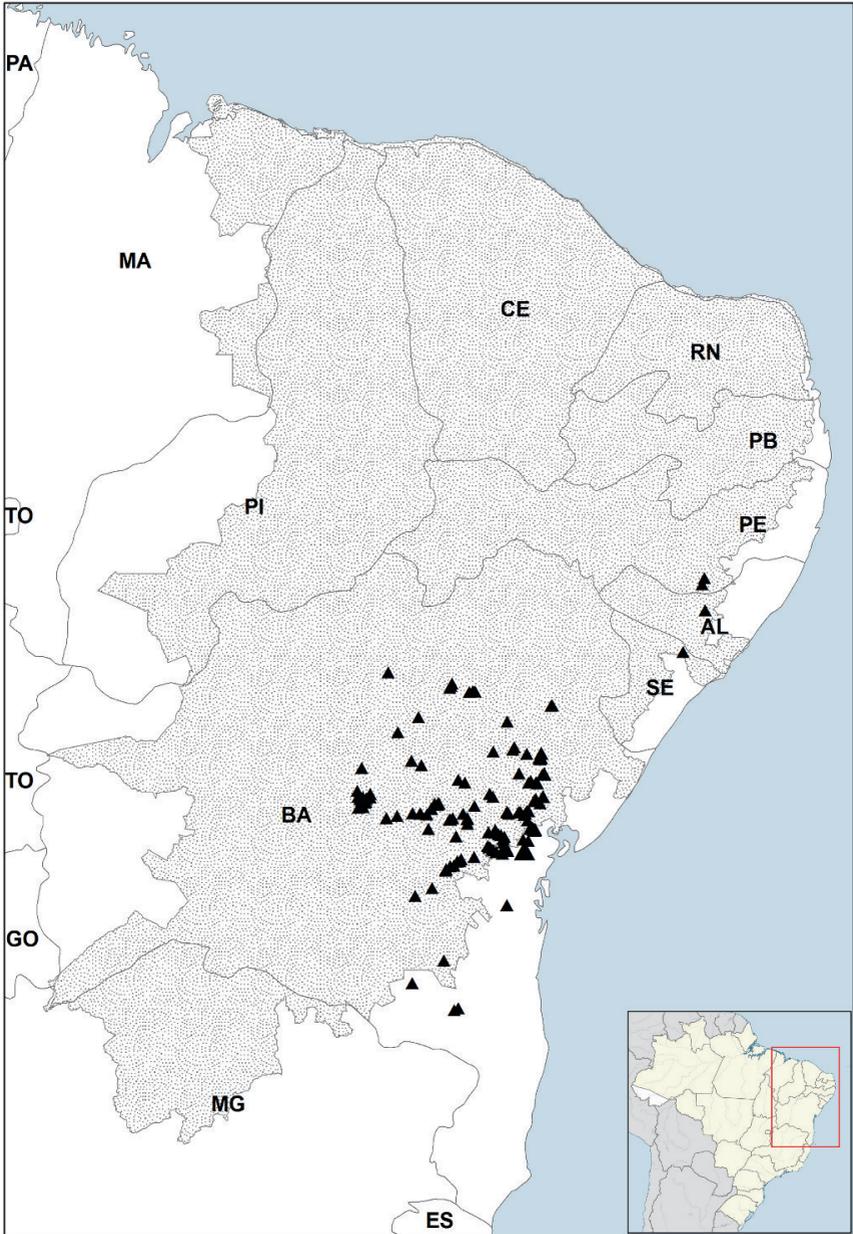


Figure 1. Map of distribution of the new species *Spondias bahiensis* (umbu-cajá). The gray area corresponds to the Brazilian Caatinga Dry Forest Biome.

Carvalho et al. 2010; Melo et al. 2012).

In spite of the numerous studies carried out so far, the origins of *umbu-cajá* and its relationships to other *Spondias* species are still poorly understood. A statement often found in the literature is that *umbu-cajá* is a hybrid between *Spondias tuberosa* and *S. mombin* (Santos et al. 2002; Santos 2003; Santos et al. 2004; Santos et al. 2005; Soares-Filho & Ritzinger 2006; Lima-Júnior et al. 2007; Fiaes et al. 2009; Gomes et al. 2009; Santos 2009a; Santos 2009b; Bastos 2010; Carvalho 2010; Carvalho et al. 2010; Ferreira 2010; Santana 2010; Santos 2010; Santos et al. 2010; Silva & Koblitz 2010; Lima et al. 2011; Barbosa et al. 2012; Lima 2012; Silva et al. 2012; Aidar et al. 2013; Santos et al. 2013). Some authors do not provide any actual data or cite references to back up this hypothesis (Santos et al. 2002; Santos et al. 2005; Lima-Júnior et al. 2007; Fiaes et al. 2009; Gomes et al. 2009; Carvalho et al. 2010; Silva & Koblitz 2010; Barbosa et al. 2012), as if the hybrid origin of *umbu-cajá* was a matter of common knowledge. Most authors cited a work by Giacometti (1993), but again this author only stated that *umbu-cajá* has a hybrid origin without providing any experimental evidence. In fact, the hypothesis of hybrid nature of *umbu-cajá* stated by the large majority of references remains untested experimentally. Only one study has tested this hypothesis, using karyological information, and the authors conclude against a hybrid origin of *umbu-cajá* (Almeida et al. 2007).

It is likely that *umbu-cajá* is presumed to be of hybrid origin due to its vernacular name, a junction of the vernacular names for *Spondias tuberosa* (*umbu*) and *S. mombin* (*cajá*). *Umbu-cajá* has this vernacular name because plants of *umbu-cajá* are similar to plants of *S. tuberosa* in the dimensions of the trees and features of the fruits, in particular the amount of pulp; but the fruits of *umbu-cajá* are comparable to those of *S. mombin* in smell and taste.

In the present study we employ both morphological and molecular analyses to investigate the relationships and similarities of *umbu-cajá* to other taxa found in Eastern Brazil, both native and introduced. Our goal is to test the hypothesis that *umbu-cajá* would be a hybrid between *Spondias tuberosa* and *S. mombin*. As a result of the combined morphometric, morphological and molecular approaches, we describe *umbu-cajá* as a distinct new species.

MATERIAL AND METHODS

Literature review — Because most of the literature about *umbu-cajá* does not distinguish between the Northern and the Bahian taxa, we made a literature review to identify the studies that have been carried out on the Bahian *umbu-cajá*. The selection of studies took into account the geographic origin of the samples analyzed, inferred from the location where the plants/fruits were collected as informed in the materials and methods sections of those studies. Since the northern *umbu-cajá* taxon is not cultivated in the state of Bahia, the studies which were carried out on plants from Bahia are assumed to have investigated the Bahian taxon. The identification of the plants was further confirmed by field trips to the collection areas mentioned in the studies, and visits to the germplasm collections of the taxon maintained at Embrapa Mandioca and Fruticultura Tropical (located in Cruz das Almas, Bahia, Brazil) and Embrapa Semiárido (located in Petrolina, Pernambuco, Brazil).

Taxon sampling and ethics statement — For the molecular analysis we sampled 67 accessions of *Spondias* (Table 2), including *S. dulcis* (5 accessions), *S. macrocarpa* Engl. (4), *S. mombin* (12), *S. purpurea* (5), the Bahian *umbu-cajá* taxon (21), *S. tuberosa* (9), and *S. venulosa* (Engl.) Engl. (11). The majority of samples were collected in the field, and for those species with a large geographical distribution we tried to collect samples from

different states in Northeastern Brazil. Collection localities, voucher information, and GenBank accession numbers are given in Table 2.

For the leaf morphometric analyses we sampled seven populations consisting of 20 individuals, of which four populations corresponded to *umbu-cajá* and one of each *S. mombin*, *S. tuberosa* and *S. venulosa*; for *S. venulosa* we only sampled ten individuals due to the difficulty in finding large populations of the species (Table 3). From each individual we collected fully expanded leaves, which were pressed and dried following usual herbarium preparation methods (Fidalgo & Bononi 1984).

All the samples used in this study were collected by the senior author and his colleagues or cooperators, and no special permissions were required for collection. Samples were collected either from public or privately owned land, and in the latter case we had the permission of the landowners to collect the samples. No collections were made in protected areas, and the field studies do not involve endangered or protected species.

Leaf morphometrics data acquisition — One mature leaf containing intact leaflets was selected from each individual for taking measurements and digitizing leaflet outlines. We measured eight leaf and two fruit characters (Figure 2), using a Vernier caliper. Leaf width was measured across the second pair of leaflets up from the base of the leaf. For leaflet outline acquisition we scanned the right side leaflets of each individual (relative to the adaxial surface of the leaf), located in the second pair up from the base of the leaf. The leaflets were positioned in the scanner with the abaxial surface facing the glass. The images obtained were edited and the petiolules erased to facilitate the detection of outlines. Two landmarks (one in the base and one in the apex), and full outlines were digitized starting from the base in a clockwise manner using TpsDig 1.40 (Rohlf 2004) and generating from 700–900 X and Y coordinates. The coordinates were entered into Morphue

al. (Slice 2002) and decomposed by Elliptic Fourier Analysis (EFA) after a Bookstein superimposition based on the basal and terminal landmarks. Only data from the outlines was used for subsequent analysis of the leaflets, and the two landmarks were used only for alignment and scale removal.

Morphometric data analyses — Initially, data from measurements and outlines was analyzed separately, using Principal Component Analysis (PCA) to detect outliers. After exclusion of outliers (20 individuals in different populations) we had a total of 110 samples remaining (15–20 individuals per population), except in the *S. venulosa* population from which we had originally 10 individuals and no outliers. Principal component analysis of all the data found little separation reflecting the large variation within groups, and for this reason we proceeded to Canonical Variates Analysis (CVA). After testing separate and combined analyses we observed the combination of traditional measurements (that reflect size and shape) and EFA coefficients (including only shape) lead to maximal separation among populations, and for this reason we present only the combined analysis in the results. Because a large number of coefficients is generated in the EFA (80 coefficients for 20 harmonics), and this would cause dimensionality problems with exaggerated group spread (Zelditch et al. 2012) when the number of samples in each group is around 20, we used the scores of the 10 Principal Components of a PCA of the EFA coefficients as input to the combined CVA, yielding therefore 18 variables (8 measurements + 10 PCs). CVA was performed taking populations as the categorical variable. The number of axes to be interpreted was chosen with the chi-square test of Bartlett (1941).

DNA extraction, amplification and sequencing — Genomic DNA was extracted using the cetyltrimethylammonium bromide (CTAB) 2× protocol (Doyle & Doyle 1987). For the genetic analyses we amplified the

Table 3. *Spondias* populations sampled for the morphometric analysis.

Species	Locality	Geographical coordinates	Voucher (HUEFS)
<i>Spondias dulcis</i>	Cruz das Almas – BA	12°39'S, 39°06'W	Carvalho, P.C.L. 29
<i>Spondias mombin</i>	Cruz das Almas – BA	12°44'S, 39°07'W	Carvalho, P.C.L. 30
<i>Spondias purpurea</i>	São Felipe – BA	12°44'S, 39°04'W	Carvalho, P.C.L. 12
<i>Spondias tuberosa</i>	Itatim – BA	12°26'S, 39°31'W	Carvalho, P.C.L. 172
<i>Spondias venulosa</i>	Amélia Rodrigues – BA	12°31'S, 38°37'W	Carvalho, P.C.L. 50
Umbu-cajá pop. 01	Lajedo Alto, Iaçú – BA	12°26'S, 39°31'W	Carvalho, P.C.L. 61
Umbu-cajá pop. 02	Serrinha – BA	11°40'S, 39°00'W	Carvalho, P.C.L. 127
Umbu-cajá pop. 03	Seabra – BA	12°30'S, 41°51'W	Carvalho, P.C.L. 145
Umbu-cajá pop. 04	Morro do Chapéu – BA	11°15'S, 40°56'W	Carvalho, P.C.L. 170

psbA-trnH intergenic spacer (Sang et al. 1997) and the *rps16* intron (Oxelman et al. 1997) from the cpDNA genome, and the external transcribed spacer (ETS) region from the nuclear encoded small subunit ribosomal DNA (SSU rDNA) using the primers ETS1F (Pell 2004) and 18S-IGS (Baldwin & Markos 1998). We used the TopTaq Master Mix Kit (Qiagen) to amplify all regions. Polymerase chain reaction (PCR) was performed in a total volume of 10 μ L containing 1 μ L (ca. 30 ng) of template DNA, 0.3 μ M of each primer, 6 μ L TopTaq mix, 2 μ L TBT (Samarakoon et al. 2013) and 0.6 μ L of water. The thermal profile for amplifying the cpDNA regions consisted of an initial denaturing step of 80°C for 5 min, followed by 35 cycles of 95°C for 1 min, 52°C for 1 min, and 65°C for 5 min, and a final extension of 65°C for 5 min. The thermal profile for amplifying the ETS region was that described by Pell (2004). To check amplification success, 1.5 μ L of each PCR product was quantified in ethidium bromide-stained 2% agarose gels. Prior to sequencing, the PCR products were cleaned using the PEG 11% (polyethylene glycol-sodium acetate method, Paithankar & Prasad 1991). DNA sequencing was performed with Big Dye 3.1 Terminator Cycle Sequencing Kit (Applied Biosystems, São Paulo, Brazil) with the same primers used for the PCR reactions. The cycle sequencing followed a program of 25 cycles of denaturation at

96°C for 10 s, annealing at 50°C for 5s, and elongation at 60°C for 4 min. Products were then sequenced using an ABI 3130XL genetic analyzer (Applied Biosystems).

Sequence edition and alignment — Electropherograms were edited and assembled using Staden Package (Staden et al. 1990) and manually aligned using Seaview 4.2.6 (Galtier et al. 1996; Gouy et al. 2010). For each region, both ends of the aligned sequences were cropped so that all accessions possessed the same sequence length. The matrices were then saved in FASTA format for further analysis.

Haplotype network estimation — We prepared cpDNA and ETS matrices containing all *Spondias* accessions, with the plastid regions manually combined into a single file (sequences of both *psbA-trnH* intergenic spacer and *rps16* intron were concatenated for each accession). The resulting matrices were input to DnaSP 5.10 (Librado & Rozas 2009), where haplotype data were generated in Roehl Data Format (.rdf) with the option of removing from analysis sites containing gaps. The .rdf files were then input to Network 4.6.1.1. (Fluxus Engineering; <http://www.fluxus-engineering.com>) to calculate and draw median-joining networks (Bandelt et al. 1999). The haplotype networks were then assembled and edited using InkScape 0.48.4 (Software Freedom Conservancy; <http://www.inkscape.org>).

Phylogeny reconstruction — In order to assess the occurrence of incongruence between the cpDNA and ETS datasets of *Spondias*, we performed phylogenetic analyses on reduced datasets consisting of “taxon genetic classes”, hereinafter TGCs (unique combinations of taxa and DNA sequences). In order to identify the TGCs, all DNA regions were manually combined into a single FASTA file (sequences of the *psbA-trnH*, *rps16* and ETS regions were concatenated for each accession). The resulting matrix was input to DnaSP 5.10 (Librado & Rozas 2009), where haplotype data was generated in Nexus format with the option of including sites containing gaps in the analysis. The haplotype identified for each accession (Table 2, column “Combined haplotype”) was then compared to the taxon to which each accession is assigned, and

unique combinations of taxa and haplotypes were given a name (Table 2, column “Taxon genetic class”). Accessions assigned to a TGC possess identical DNA sequences. A total of 18 TGCs were identified, and these were used as terminals for the phylogenetic analyses. Two matrices were prepared, one consisting of ETS sequences from each TGC, and a second matrix consisting of the combined *psbA-trnH* and *rps16* sequences from each TGC. The two cpDNA regions were combined in tree reconstructions since the entire chloroplast genome is regarded as being a single linkage group and thus all cpDNA regions are expected to exhibit the same phylogenetic pattern (Doyle 1992). The single TGC for the introduced species *Spondias dulcis* was used as outgroup in the phylogenetic analyses. From the maximum

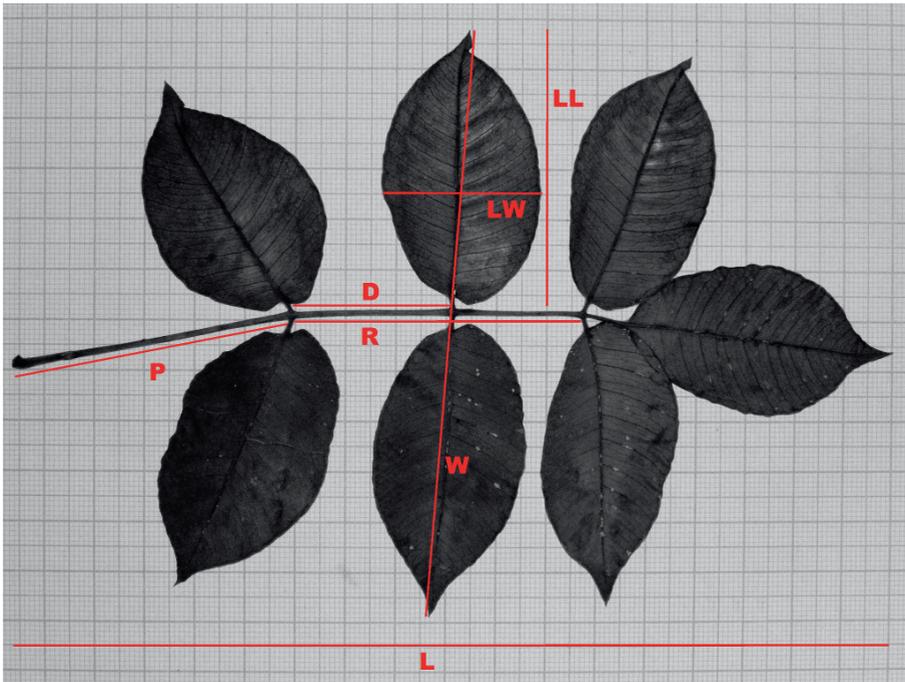


Figure 2. Leaf measurements used in the morphometric analysis. **L.** Leaf length; **W.** Leaf width; **P.** Petiole length; **D.** Distance between first and second leaflet pairs; **LL.** Leaflet length; **LW.** Leaflet width; **R.** Rachis length. Other characters measured (not in the picture): **N.** Number of leaflets; **FL.** Fruit length; **FW.** Fruit width.

parsimony analyses of the cpDNA and ETS datasets we generated 80% majority rule consensus trees (one from each dataset), which were plot facing each other in R version 3.1.1 (Ihaka & Gentleman 1996; R Core Team 2014) using the function *cophyloplot* of the package *APE* version 3.1-4 (Paradis et al. 2004). The resulting graphic image was saved as a PDF file containing the image in vector format and then edited using *InkScape* 0.48.4.

We also prepared an expanded cpDNA dataset for use in the divergence time estimation analysis. This dataset included one sequence of each distinct cpDNA haplotype identified for *Spondias*, and sequences from species of other genera of Anacardiaceae and also from genera of Burseraceae which were used as outgroups in the analyses (Table 4). For the assessment of support values for the clades recovered in the chronogram generated by the divergence time estimation analysis, we carried out maximum parsimony and Bayesian inference phylogenetic analyses using the same dataset.

Datasets were analyzed using maximum parsimony as optimality criterion in PAUP* 4.0b10 (Swofford 2002), and using Bayesian inference in MrBayes version 3.2.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Parsimony analysis was performed using a heuristic search to generate 10,000 replicates of random taxon addition using equal (Fitch) weights and TBR, 10 trees held at each step, MulTrees off, saving only the shortest trees or the shortest from each replicate. The resulting trees were used as starting points in another round of TBR with MulTrees on. In the analyses presented here, gaps were treated as missing data, poly repeats were included, and branches with a minimum length of zero were collapsed. Support for tree topology was evaluated with 2,000 bootstrap (BS) replicates in PAUP* 4.0b10 (TBR, 10 trees held at each step, MulTrees on). For the Bayesian inference analyses, an appropriate nucleotide substitution model was identified

using a hierarchical likelihood-ratio test implemented in Modeltest 3.7 (Posada & Crandall 1998) for selection of the best-fit models for the different partitions of the data. The MCMC algorithm was run for 10,000,000 generations with two runs of four chains (three hot and one cold chain), starting from random trees and sampling one out of every 1,000 generations. The first 25% of trees (burn-in) were excluded to avoid trees that might have been sampled prior to convergence of the Markov chains, and a majority-rule consensus tree was calculated for the remaining trees. The posterior probability of each topological bipartition was estimated by the frequency of these bipartitions across all trees sampled. Clades with posterior probabilities higher than 95% were considered well supported.

Calibration and divergence time estimation— In order to estimate absolute divergence times within *Spondias* we obtained from GenBank sequences of the plastid *psbA-trnH* intergenic spacer and *rps16* intron regions from species of other genera of Anacardiaceae and Burseraceae which were used as outgroups in the dating analyses (Table 4). We generated a maximum clade credibility (MCC) chronogram to estimate absolute divergence times within *Spondias* and outgroup taxa, using a combined cpDNA matrix with a reduced sampling of *Spondias* that only included sequences of the previously identified haplotypes. We used previously estimated ages for Burseraceae and Anacardiaceae and fossil records to set age constraints on this new phylogeny. A combination of fossil and secondary calibrations with a relaxed molecular clock approach was employed to simultaneously estimate phylogenies and divergence times in the face of uncertainty in phylogenetic relationships, evolutionary rates, and calibration times using BEAST v1.8 (Drummond et al. 2012). We assigned an age constraint on the most recent common ancestor (MRCA) of all taxa within Burseraceae and Anacardiaceae using

a normally distributed calibration prior with the mean 70.0 Million years before present (Ma) and standard deviation 7.07 Ma (Xie et al. 2014). For Burseraceae we assigned an age constraint for the MRCA of all taxa within the family using a normally distributed calibration prior with the mean 64.92 Ma and standard deviation 6.61 Ma, and age constraints for MRCA of two internal nodes, the *Bursera* clade using a normally distributed calibration prior with the mean 49.43 Ma and standard deviation 5.94 Ma, and the *Bursera-Commiphora* split using a normally distributed calibration prior with the mean 54.75 Ma and standard deviation 5.9 Ma (De-Nova et al. 2012). In Anacardiaceae, calibration points from fossil records were used for constraining the stem age of the *Anacardium* clade using a lognormally distributed calibration prior with the parameters mean 11.9, log (Stdev) 0.4, and offset 37.2 (placing its age 61.26 to 42.22 Ma) with basis in an *Anacardium* fossil described by Manchester et al. (2007); and the stem age of the *Spondias* clade using a lognormally distributed calibration prior with the parameters mean 8.25, log (Stdev) 0.4, and offset 11.6 (placing its age 15.08 to 28.28 Ma) with basis in a *Spondias* fossil described by Herrera et al. (2012a; 2012b). Secondary calibration points in Anacardiaceae were assigned as follows: for

the MRCA of all taxa of Anacardiaceae we used a normally distributed calibration prior with the mean 60.0 Ma and standard deviation 4.24 Ma (Nie et al. 2009); for the MRCA of internal nodes *Mangifera-Anacardium* split we used a normally distributed calibration prior with the mean 56.07 Ma and standard deviation 5.66 Ma (Xie et al. 2014); for the MRCA of the *Choreospondias-Harpephyllum* split we used a normally distributed calibration prior with the mean 55.8 Ma and standard deviation 4.5 Ma. The best fit model for each region was identified with the Akaike Information Criterion (AIC) (Posada & Buckley 2004) implemented in Modeltest 3.7 (Posada & Crandall, 1998) and for both the regions was estimated the GTR model with Gamma distribution. Posterior distributions of parameters were approximated using a MCMC analyses of 50,000,000 generations. Convergence of the chains was checked using the program Tracer 1.6 (Rambaut et al. 2013), the first 25% of trees were discarded as burn-in, and the remaining trees were combined using LogCombiner v.1.6.2 (Drummond et al. 2012). The maximum clade credibility tree (MCCT) used for the analysis was calculated using TreeAnnotator v.1.6.2 (Drummond et al. 2012) to summarize ages and the posterior probability distribution of chronograms. The

Table 4. Species from genera of Anacardiaceae and Burseraceae which were used as outgroups in the dating analyses, and their GenBank Accession numbers for the *rps16* intron and *trnH-psbA* intergenic spacer regions of the plastid genome.

Taxon	Family	<i>rps16</i> Genbank Accession Number	<i>trnH-psbA</i> Genbank Accession Number
<i>Anacardium excelsum</i> (Bertero & Balb. ex Kunth) Skeels	Anacardiaceae	KF664443	KF664314
<i>Anacardium occidentale</i> L.	Anacardiaceae	KF664442	KF664313
<i>Choreospondias axillaris</i> (Roxb.) B.L. Burtt & A.W. Hill	Anacardiaceae	AY594591	HQ427035
<i>Harpephyllum caffrum</i> Bernh.	Anacardiaceae	AY594601	KF664318
<i>Mangifera indica</i> L.	Anacardiaceae	AB598025	JX856904
<i>Beiselia mexicana</i> Forman	Burseraceae	AY314997	JF919222
<i>Boswellia sacra</i> Flueck.	Burseraceae	AJ416489	JF919223
<i>Bursera microphylla</i> A. Gray	Burseraceae	AY309289	AY309396
<i>Bursera graveolens</i> (Kunth) Triana & Planch.	Burseraceae	GQ505922	GQ505924
<i>Canarium pilosum</i> A.W. Benn.	Burseraceae	AY315008	AY635378
<i>Canarium vulgare</i> Leenh.	Burseraceae	AY315009	AY635381
<i>Commiphora franciscana</i> Capuron	Burseraceae	AY315014	KF035037
<i>Commiphora monstrosa</i> (H. Perrier) Capuron	Burseraceae	AY831956	KF035045
<i>Protium apiculatum</i> Swart	Burseraceae	AJ416484	GQ428754
<i>Protium madagascariense</i> Engl.	Burseraceae	AY315029	FJ466490
<i>Tetragastris altissima</i> (Aubl.) Swart	Burseraceae	AY315032	GQ428760
<i>Tetragastris panamensis</i> (Engl.) Kuntze	Burseraceae	AY594640	GQ982384

majority rule consensus tree was viewed and edited on FigTree 1.4.2 (Rambaut 2014). The resulting graphic image was saved as a PDF file containing the image in vector format and then edited using InkScape 0.48.4.

Nomenclature — The electronic version of this article in Portable Document Format (PDF) in a journal with an ISSN or ISBN will represent a taxonomically valid publication according to the International Code of Nomenclature for algae, fungi, and plants (Knapp et al. 2011). Hence, the new names contained in the electronic publication of a article are effectively published under that Code from the electronic edition alone, so there is no longer any need to provide printed copies.

RESULTS

Morphometric data analyses — Only the first two axes of the CVA are worth interpreting, and they accounted for 89.1% of the variance among population centroids (Figure 3). CV1 (69.1% of variance) was very significant (chi-square = 344.66, $p < 0.000001$) as well as CV2 (19.6% of variance, chi-square = 163.91, $p < 0.000001$). Third axis (chi-square = 73.39, $P = 0.1973$) and subsequent axes (values not shown) did not present significant deviation from random patterns. The first CV concentrates most of the differences among species, whereas the second corresponds mostly to within-population variation. In the former we have an opposition from *S. mombin* at the left side, and *S. tuberosa* at the right, and *S. venulosa* in intermediate position closer to *S. mombin*. This is due mainly to differences in leaf size and number of leaflets (this axis was negatively correlated with all traditional measurements [data not shown]). Considering only the leaf morphology analyzed in our study, all species display some degree of overlap. Regarding *umbu-cajá*, all populations were clustered in intermediate positions between *S. venulosa* and *S. tuberosa*, with

moderate overlap in leaf morphology with these two species. There is a slight tendency that *umbu-cajá* overlaps more with *S. tuberosa*, especially the Serrinha population.

Haplotype network estimation — Figure 4 depicts the haplotype networks reconstructed for the combined cpDNA regions (67 *Spondias* accessions) and the nuclear ETS region (65 accessions). Haplotypes identified for each accession are listed in Table 2. In the cpDNA network, no haplotypes were found to be shared by distinct species, with each species possessing a distinct set of haplotypes. Three haplotypes each were identified for *S. mombin* and *S. venulosa*, two haplotypes for *umbu-cajá*, and one haplotype for each of the remaining species. The distribution of haplotypes of *S. mombin* is not correlated with geography, whereas haplotypes of *S. venulosa* are geographically distributed, with haplotype H_10 occurring in the states of Bahia and Espírito Santo, and haplotypes H_11 and H_12 occurring in the state of Rio de Janeiro. A geographic correlation is also found between the haplotype of *S. venulosa* most closely related to *umbu-cajá* and both haplotypes of *umbu-cajá*, which are all found in the state of Bahia. The smallest genetic distance connecting two taxa is observed between *S. venulosa* and *umbu-cajá*, with a minimum of two mutational steps separating them. *Spondias tuberosa* is found to be a minimum of six mutational steps apart from *S. venulosa*, and a minimum of eight mutational steps apart from *umbu-cajá*. These three taxa are most closely related to each other than to any other species, with a minimum of 15 mutational steps separating either *S. venulosa* or *S. tuberosa* from *S. purpurea*, 16 from *S. dulcis*, and 17 from *S. macrocarpa*. The largest genetic distance separating two taxa is observed between *S. mombin* and both *S. venulosa* and *S. tuberosa*, with a minimum of 27 mutational steps separating the first taxon from either of the latter.

In the ETS network, all accessions of both *umbu-cajá* and *Spondias tuberosa* share the same

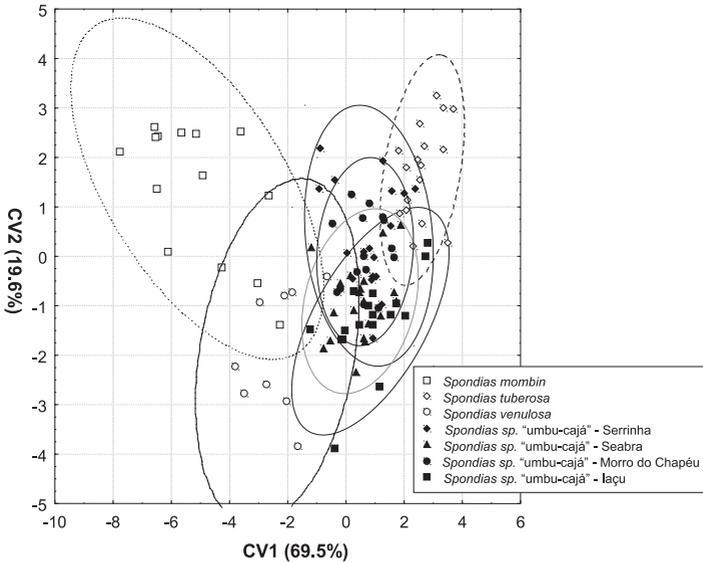


Figure 3. Plot of the first and second axes of Canonical Variates Analysis (CVA) of the morphometric data.

haplotype H_01. Each of the remaining species has its own set of haplotypes, without haplotypes being shared between distinct species. Four haplotypes are identified for *S. mombin*, three haplotypes for *S. macrocarpa*, two haplotypes for *S. venulosa*, and one haplotype for each of the remaining species. The distribution of haplotypes of *S. mombin* is not correlated with geography, whereas haplotypes of *S. venulosa* are geographically distributed, with haplotype H_11 occurring in the states of Bahia, and haplotype H_12 occurring in the states of Espírito Santo and Rio de Janeiro. The smallest genetic distance connecting distinct taxa is observed between haplotype H_12 of *S. venulosa* and haplotype H_01 shared by *S. tuberosa* and *umbu-cajá*, with a minimum of nine mutational steps separating these taxa. These three taxa are most closely related to each other than to any other species. The largest genetic distance is observed between haplotypes belonging to *S. macrocarpa*, with 54 mutational steps separating haplotype H_05

from haplotype H_04, and 57 mutational steps separating haplotype H_05 from haplotype H_03.

Phylogeny reconstruction—Figure 5 shows the resulting cpDNA and ETS consensus trees including all TGCs. For all recognized species, TGCs belonging to the same species were grouped in the same clade, except for *S. macrocarpa* in the ETS tree, on which the species' TGCs did not form a clade. TGCs belonging to *umbu-cajá* are grouped in a well-supported clade in the cpDNA phylogeny, but this clade is placed in an unresolved polytomy with the TGCs belonging to *S. venulosa*. In the ETS phylogeny, TGCs belonging to *umbu-cajá* are placed in an unresolved polytomy together with the TGCs belonging to *S. tuberosa*.

Divergence time estimation—Figure 6 shows the chronogram resulting from the dating analysis. The crown age of *Spondias* is dated at 20.3 Ma, with a first dichotomy between the Asian *Spondias dulcis* and a clade

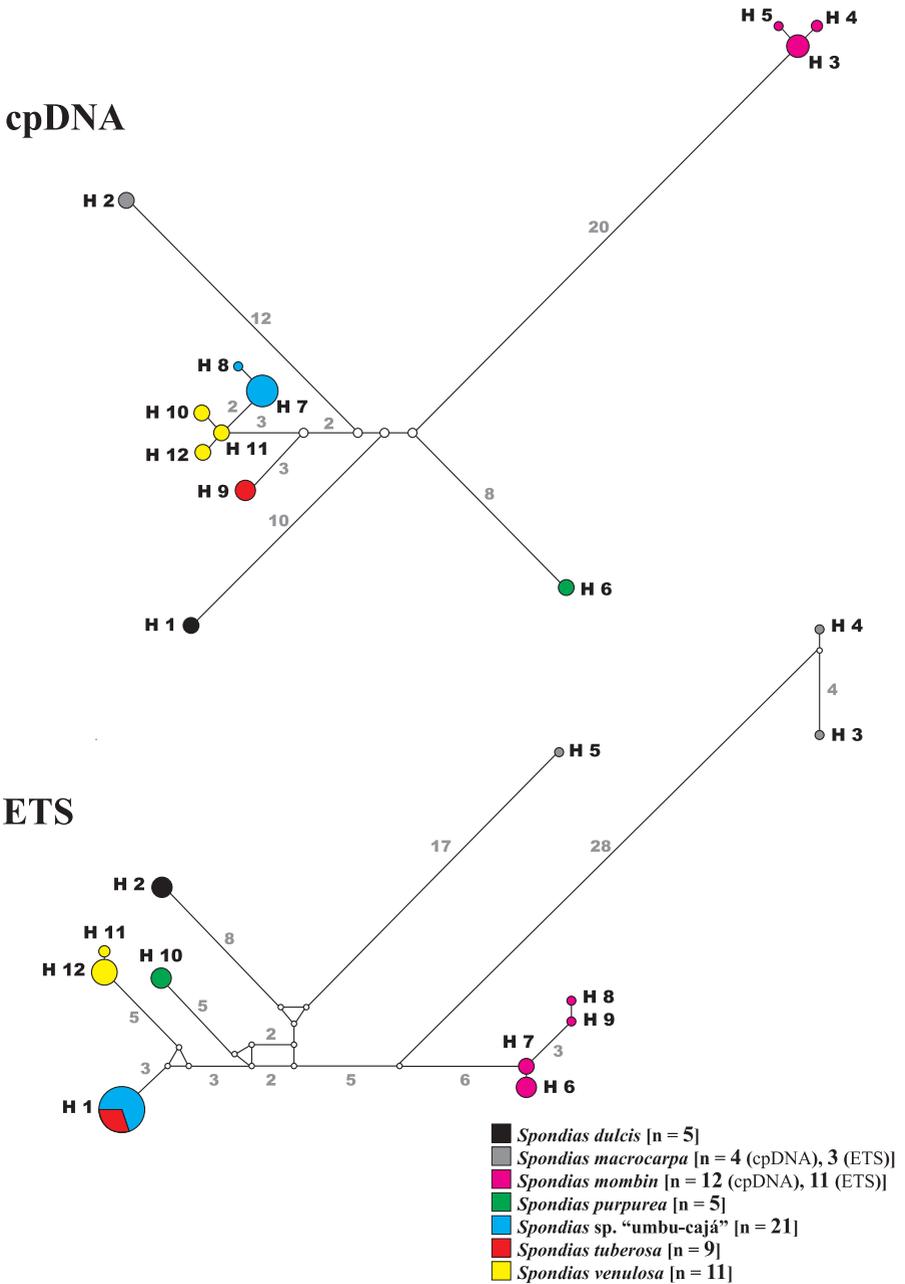


Figure 4. Haplotype networks of *Spondias* reconstructed from the combined *psbA-trnH* and *rps16* cpDNA regions, and the nuclear ETS region. **n** = number of accessions for each taxon. See Table 2 for more information about accessions.

including all Neotropical species. The first divergence within the Neotropical clade, dated 16.64 Ma, is between a clade comprising *S. mombin* and *S. purpurea*, and a clade comprising *S. macrocarpa*, *S. tuberosa*, *umbu-cajá* and *S. venulosa*. The divergence between *S. mombin* and *S. purpurea* is dated at 13.06 Ma, and the crown age for haplotypes belonging to *S. mombin* is dated at 3.2 Ma. *Spondias macrocarpa* diverged 13.33 Ma from a clade comprising *S. tuberosa*, *umbu-cajá* and *S. venulosa*. Within the latter clade the first divergence, dated 8 Ma, is between *S. tuberosa* and a clade consisting of *umbu-cajá* and *S. venulosa*. The divergence between *umbu-cajá* and *S. venulosa* occurs at 3.79 Ma, with crown ages of *umbu-cajá* and *S. venulosa* respectively 0.97 and 2.3 Ma ago.

DISCUSSION

The origins of umbu-cajá—The hypothesis that the Bahian *umbu-cajá* is of hybrid origin between *Spondias mombin* and *S. tuberosa* is refuted in both molecular and morphological analyses. As well as being morphologically distinct from *S. mombin* (Figure 3), *umbu-cajá* is also genetically and phylogenetically fairly removed from it (Figures 4, 5, 6). The closest relatives of *umbu-cajá* are *Spondias venulosa* and *S. tuberosa* (Figures 4, 5, 6). *Umbu-cajá* differs from *S. venulosa* by only two mutational steps in the cpDNA haplotype network (Figure 4), and in the ETS haplotype network *umbu-cajá* shares the same haplotype with *S. tuberosa* (Figure 4).

Spondias tuberosa, popularly known with the vernacular names of *umbu* or *imbu*, is a species endemic to the Brazilian semi-arid region which is widely distributed throughout the states of Northeastern Brazil and also occurs in the North of Minas Gerais, being a very typical element of the dry deciduous vegetation of the *Caatinga* biome (Carvalho 2006; Lorenzi et al. 2006; Santos et al. 2008a; Araújo 2010). The species

has great cultural and economic importance, being deeply rooted in the imaginary of peoples from Northeast Brazil as inferred by the many examples of poetry, short stories and popular songs with references to the species, which is viewed as a life-giving tree and a symbol of endurance due to it reliably fruiting even during the harshest of the periodic droughts that plague Northeastern Brazil. Trees of this species are often spared in areas where the original vegetation is cleared for agriculture because the edible fruits of *S. tuberosa* are much valued due to its thick, acidic, juicy mesocarp. Fruits of the species constitute a major source of income for many families at the time of harvest: according to IBGE (1997-2011), in the 15-year period from 1997 to 2011 there were marketed an average of 9,674.8 tonnes of *Spondias tuberosa* fruits per year, with the vast majority of this production still being obtained from extractivism in natural tree stands.

Spondias venulosa occurs in semi-deciduous forests and its distribution encompasses the states of Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro. Although the species can be locally abundant, especially in Espírito Santo and Rio de Janeiro, it does not seem to be very common elsewhere. In Bahia, large populations of the species are rare: usually only single trees or at most small groups are found scattered in habitat, in particular towards the central regions of the state. The past distribution and abundance of the species is unknown due to most of its forest habitats having been destroyed, producing the rather fragmented distribution it currently displays. *Spondias venulosa* is generally not cultivated because its fruits are rather fibrous, with scant mesocarp, and very sour.

Umbu-cajá is so far only known from cultivation: unquestionably natural populations have not yet been located, and plants of this taxon are always found in human-modified environments, usually near houses and in farms, indicating *umbu-cajá*'s dependence on

cpDNA

ETS

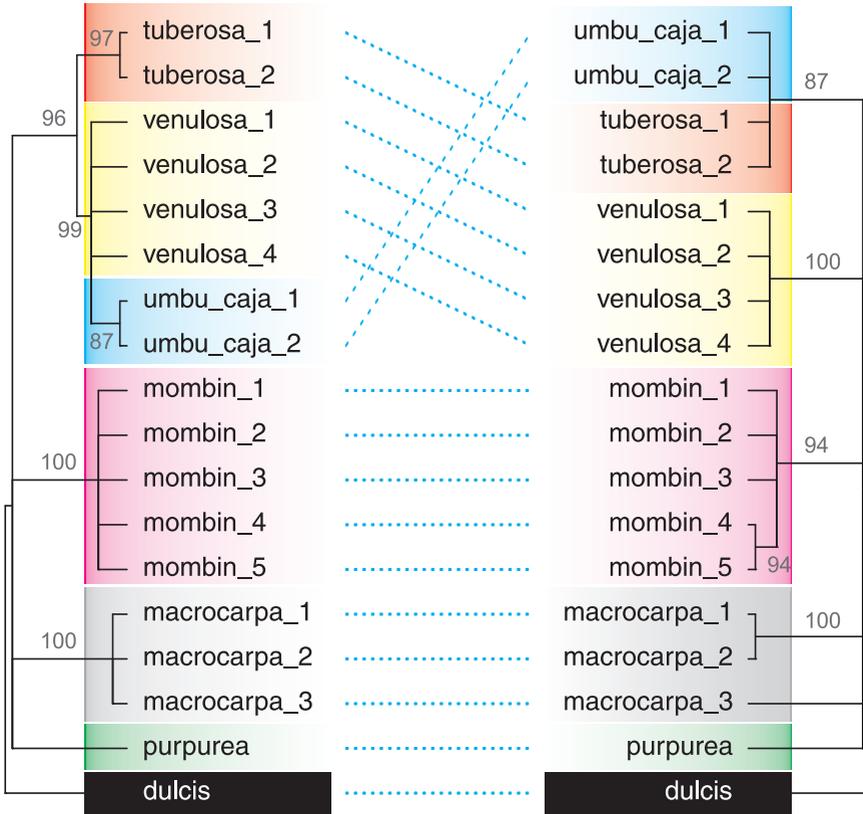


Figure 5. Contrasting phylogenetic relationships in *Spondias* as reconstructed from the combined *psbA-trnH* and *rps16* cpDNA regions, and the nuclear ETS region. Numbers above branches are bootstrap support values.

humans for its propagation and dispersion (Carvalho 2006; Soares-Filho 2011). Given the small genetic distance between *umbu-cajá* and *S. venulosa* in the cpDNA haplotype network (Figure 4) and in the phylogenetic analysis of the cpDNA dataset (Figure 5), and also the fact that *umbu-cajá* groups with *S. tuberosa* in both the ETS haplotype network (Figure 4) and the phylogenetic analysis of the ETS dataset (Figure 5), a feasible hypothesis is that *umbu-cajá* could be a domesticated form of either *S. tuberosa* or

S. venulosa, that was brought into cultivation by man.

However, despite the short genetic distance between *umbu-cajá* and *S. venulosa* in the cpDNA haplotype network, an indication that they have distinct gene pools derives from the fact that samples of *S. venulosa* collected in the states of Bahia and Rio de Janeiro (a distance of over 1,200 km; Table 2) are genetically closer to each other than samples of *umbu-cajá* and *S. venulosa* collected in Bahia. *Umbu-cajá* has the same haplotype as

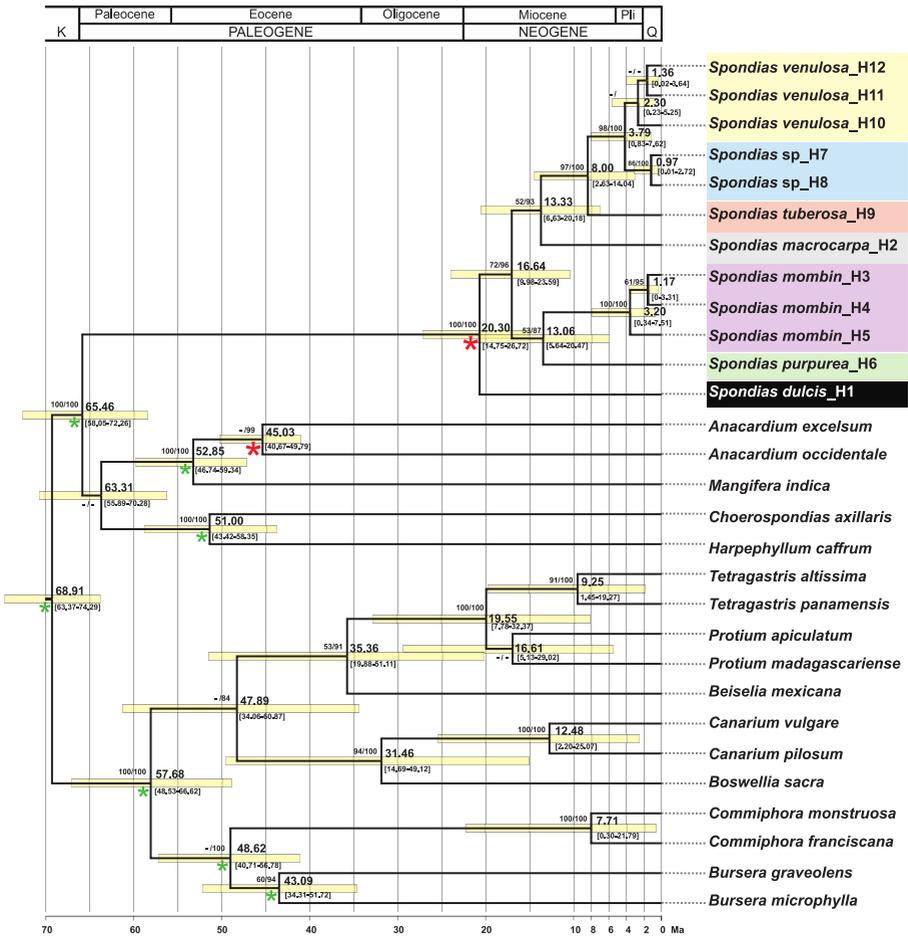


Figure 6. Chronogram displaying divergence times in *Spondias* and related taxa with basis on the combined *rps16* and *trnH-psbA* datasets. Nodes marked with green asterisks (*) were calibrated using secondary age constraints, nodes marked with red asterisks (*) were dated using fossil age constraints. All *Spondias* species are represented by different colors, with co-specific haplotypes having the same color. Acronyms of the unique haplotypes used as terminals are placed after the names of accessions. Q: Quaternary; Pli: Pliocene; K: Cretaceous. 95% HPD (highest posterior density) confidence intervals are shown as bars at each node.

S. tuberosa in the ETS haplotype network, but it is genetically removed from *S. tuberosa* in the cpDNA haplotype network (Figure 4). More importantly, *umbu-cajá* has a number of morphological features that readily distinguish it from both *S. venulosa* and *S. tuberosa* (Table 5).

The fact that *umbu-cajá* appears to occur exclusively cultivation does not necessarily mean that the differences observed between this taxon and both *S. venulosa* and *S. tuberosa* are entirely due to changes that occurred during the process of *umbu-cajá* domestication. *Umbu-cajá* could be a naturally

occurring taxon whose original habitats were greatly modified by man, which coupled with *umbu-cajá* having been taken to cultivation have obscured the origins of this taxon. Given the current distribution of cultivated *umbu-cajá*, if it was a naturally occurring taxon then the two possible biomes where it could have originally occurred are the inland *Caatinga* characterized by possessing semiarid vegetation, and the moister Atlantic Forest located nearer to the coast. Of these, the *Caatinga* is better preserved and large areas of original vegetation still exist. However, *umbu-cajá* is not found occurring naturally in the *Caatinga*, which is inhabited exclusively by *Spondias tuberosa*.

The Atlantic Forest biome comprises different physiognomies ranging from moist forests closer to the ocean, to semi-deciduous and deciduous forests further inland which intergrade with the semiarid vegetation of the *Caatinga*. It is possible that *umbu-cajá* originally inhabited drier phases of the Atlantic Forest biome in the state of Bahia. However, only about 11.4 percent of the Atlantic Forest remain in Bahia (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais - INPE 2014), and the drier, deciduous and semi-deciduous forests are virtually gone (a map can be consulted online at <http://mapas.sosma.org.br/>). It is not difficult to find trees of *umbu-cajá* in the middle of fields and pastures, but there is no way of telling if these plants were planted or if they were left standing when the original vegetation was removed.

Spondias venulosa also inhabits areas of semi-deciduous to deciduous forests, but this species is uncommon in the state of Bahia, probably because the original vegetation where the species occurred has been almost completely eradicated. Our collections of the species consisted mostly of isolated trees found in managed landscapes – in fields, pastures, or near roadsides. These isolated *S. venulosa* trees can be more straightforwardly interpreted as trees left standing when the

original vegetation was removed, since the species is not usually cultivated. This contrasts with the situation of *umbu-cajá*, where trees in the same conditions cannot be automatically interpreted as left standing precisely because this taxon is widely cultivated.

Plants of *umbu-cajá* can sometimes be found growing in sympatry with *S. venulosa* or more frequently with plants of *S. tuberosa*, with the latter being cultivated, or consisting of wild plants tolerated in the managed landscapes, or wild plants occurring in natural vegetation. No instance of sympatry between the three taxa has so far been recorded. The occurrence of sympatry between *umbu-cajá* and either *S. tuberosa* or *S. venulosa* is often due to individuals of these species being spared in areas where the original vegetation in which they occurred was cleared for agriculture, followed by introduction of *umbu-cajá* in these areas.

It is possible that *umbu-cajá* could have originated from hybridization between *Spondias tuberosa* and *S. venulosa*. In spite of the morphological features that distinguish *umbu-cajá*, *S. tuberosa* and *S. venulosa*, there is overlap in leaf morphometric characters between all three taxa (Figure 3). Moreover, the incongruous placement of *umbu-cajá* in the different genomic compartments, with *umbu-cajá* positioned nearer to *S. venulosa* in the plastid cpDNA dataset and nearer to *S. tuberosa* in the nuclear ETS dataset, also gives support to the hypothesis of hybrid origin. *Spondias tuberosa* and *S. venulosa* are currently ecologically confined to different habitats and do not occur in sympatry, although the two taxa could have come in contact during past climatic changes (Behling et al. 2000; Pennington et al. 2000; Auler et al. 2004a, 2004b), making possible the hybridization events that gave rise to *umbu-cajá*. Alternatively, *umbu-cajá* could be a human-mediated hybrid originating from man bringing into sympatry the previously separated wild progenitor species *S. venulosa* and *S. tuberosa*. The genesis of *umbu-cajá*

might not be contemporary because it possesses cpDNA haplotypes which are distinct from those found in both *S. venulosa* and *S. tuberosa* – if *umbu-cajá* is a recent hybrid, either natural or the result of human intervention, then it conceivably should possess haplotypes identical to those of one or both parental species.

Are the genetic distances between *umbu-cajá* and related species meaningful? If the divergence times between haplotypes of *umbu-cajá*, *S. tuberosa* and *S. venulosa* would fall within the Holocene — the epoch from about 11,700 years ago to the present (Walker et al. 2009), a period when humans were unquestionably present in the Americas and when the majority of plant domestication took place (Piperno 2011) — then the hypothesis of *umbu-cajá* being the product of human intervention cannot be falsified. But if divergence times are dated from older than the Holocene then *umbu-cajá* is more likely a naturally occurring taxon. In order to address this question we reconstructed and dated a phylogeny including sequences of the different cpDNA *Spondias* haplotypes and also sequences of other genera of Anacardiaceae and Burseraceae as outgroups (Figure 6). We found that *umbu-cajá* diverged from *S. venulosa* at least 3.79 million years ago; even taking in account the 95% probability range (0.83 to 7.62 Ma ago), the minimum divergence time between *umbu-cajá* and *S. venulosa* of over 830,000 years ago is still much older than the human colonization of the Americas during the Holocene. It is thus improbable that *umbu-cajá* is a product of hybridization between *S. tuberosa* and *S. venulosa* derived from human interventions, by bringing *S. tuberosa* and *S. venulosa* together by cultivation of these species and/or habitat disturbance.

There is further evidence against the hypothesis of a recent hybrid origin for *umbu-cajá* (Almeida et al. 2007): it was found to be diploid like all *Spondias* examined so far, including *S. pinnata* (Banerji 1936; Mehra 1976; Sarkar et al. 1982;

Singhal & Gill 1990), *S. mombin* (Guerra 1986; Almeida et al. 2007), *S. tuberosa* (Pedrosa et al. 1999; Almeida et al. 2007), *S. dulcis* (Almeida et al. 2007), *S. purpurea* (Almeida et al. 2007), and *S. venulosa* (Almeida et al. 2007). *Umbu-cajá* was also discovered to possess a distinctive karyotype with exclusive CMA banding patterns, not heteromorphic or intermediate between those of the other species examined, or specifically between *S. tuberosa* and *S. mombin* or *S. venulosa* (Almeida et al. 2007).

A statement often found in the literature is that sexual propagation of *umbu-cajá* is not practical because most endocarps do not possess viable seeds (Soares-Filho & Ritzinger 2006; Carvalho et al. 2008; Fiaes et al. 2009; Santos 2009b; Santos 2009a; Bastos 2010; Carvalho 2010; Santos 2010; Santana et al. 2011a; Santana et al. 2011b; Soares-Filho 2011; Lima 2012). Some authors do not cite references (Soares-Filho & Ritzinger 2006; Bastos 2010; Soares-Filho 2011), while the remaining authors cite the works of Souza and collaborators (Souza et al. 1997; Souza 1998). However, these studies were carried out on the Northern *umbu-cajá* taxon, not the Bahian *umbu-cajá*. The Bahian *umbu-cajá* produces a high percentage of viable seeds (Ritzinger et al. 2008) which germinate readily (Machado, pers. obs.). Although the propagation of favored genotypes is asexual by means of large stem-cuttings (Carvalho et al. 2008), sexual reproduction also occurs: seedlings growing near houses have been observed at a number of places (Machado, pers. obs.), and when questioned about the origin of the plants found in their land, landowners have often stated that the plant “just grew there” (Machado, pers. obs.), suggesting volunteer seedlings establishment by endocarps discarded after consumption of fruits by man and domestic animals.

Umbu-cajá also exhibits high levels of phenotypic variability among different

accessions (Carvalho 2006; Ritzinger et al. 2008; Santos et al. 2008b; Carvalho et al. 2008; Santos 2009a; Santos et al. 2009; Santana et al. 2010; Santos 2010; Lima 2012; Santos et al. 2012) as well as considerable genetic diversity (Santana et al. 2010; Santos 2010; Santana 2010; Santana et al. 2011b). The high genetic diversity observed in *umbu-cajá* is probably due to this taxon being under a more informal domestication regimen – although plants with more desirable features are vegetatively propagated, volunteer seedlings are often tolerated and allowed to grow.

Distinguishing features of umbu-cajá — Table 5 summarizes the main features of *umbu-cajá* that distinguish it from both *S. tuberosa* and *S. venulosa*. *Umbu-cajá* is a small tree 4 to 8 meters tall, with an umbrella-shaped canopy 6 to 12 meters in diameter (Figure 7B), although the plant can attain larger dimensions when growing in more humid environments (Santos et al. 2009). *Umbu-cajá* is a larger tree than *S. tuberosa*, which reaches 3 to 5 meters in height (Figure 7A), but it is smaller than *S. venulosa*, which usually can reach 6 to 20 meters in height (Figure 7C). The canopy of *S. tuberosa* is also umbrella-shaped (Figure 7A), whereas in *S. venulosa* it is funnellform or shaped like an inverted-cone (Figure 7C). To our knowledge, there is no canopy management in these taxa — we did not find any references in the literature and we also did not observe evidence of pruning in the trees we sampled. Therefore, we assume their canopy shapes as being natural, although their shape could be the result of environmental influence — plants growing in more open environment developing an umbrella-shaped canopy, whereas plants growing in more dense vegetation possessing a funnellform canopy. Branching patterns also differ among the three taxa: *S. tuberosa* is very densely branched, with crooked branches; *umbu-cajá* is less densely branched and branching is not crooked; and *S. venulosa* has a more open canopy (Figure 7). Also, *umbu-cajá* and *S.*

venulosa have single trunks, unlike *S. tuberosa* that often has multiple trunks or branches very close to the base (Figure 7). The bark of *umbu-cajá* is smooth, whereas in *S. tuberosa* the bark is either smooth or shed in small flakes, and it is shed in rectangular plates in *S. venulosa*.

The phenology of *umbu-cajá* differs from both *S. tuberosa* and *S. venulosa*. *Umbu-cajá* flowers in November and December, at the start of the Summer rainy season. Flowers are produced with the plants fully leafed, and fruits ripen from February to March. *Spondias tuberosa* flowers earlier, in September and October. Flowers appear before leaf flush, and the plants bear fruits in December and January. *Spondias venulosa* flowers from December to February, and fruits are ripe from August to October.

All three taxa broadly overlap in leaf (and leaflet) dimensions, shape, and number of leaflet pairs; however, leaves of *S. tuberosa* are in the lower end of the range, whereas leaves of *S. venulosa* are at the upper end, with leaves of *umbu-cajá* occupying an intermediate position. The intermediacy in leaf characters observed in *umbu-cajá* could be interpreted as indicative of hybrid origin, but it could also be explained as the result of ecological adaptation to different environmental conditions. Species inhabiting more xeric habitats such as *S. tuberosa* and *S. purpurea* possess reduced leaves, whereas species inhabiting more mesic environments, such as *S. venulosa* and *S. mombin*, possess larger leaves. Furthermore, in the leaf morphometric analysis the degree of overlap between *S. bahiensis* and either *S. venulosa* and *S. tuberosa* is not higher than between other established species considered as different taxa (e.g. the overlap between *S. mombin* and *S. venulosa*).

Umbu-cajá, *S. tuberosa* and *S. venulosa* can all be identified using simple qualitative leaf characters (Figure 8). The morphology and indumentum of leaflets are very characteristic for each of them. *Umbu-cajá* has leaflets with margins at base curved towards the abaxial

Table 5. Morphological characteristics distinguishing *Spondias tuberosa*, the new species *S. bahiensis* (umbu-cajá), and *S. venulosa*

Character	<i>Spondias tuberosa</i>	<i>Spondias bahiensis</i>	<i>Spondias venulosa</i>
Tree height	3–5 m	4–8 m	6–20 m
Trunk height before branching	branching at base or if single usually less than one meter tall	single, one to two meters tall	single, two or more meters tall
Bark	smooth or shed in small flakes	smooth	corky, shed in rectangular plates
Crown shape	umbrella-shaped	umbrella-shaped	funneliform
Branching pattern	densely branched, with crooked branches	less densely branched	less densely branched
Margin of leaflet at base	flat	curved towards abaxial surface	revolute towards abaxial surface
Trichomes along leaflet margins	distributed along the entire leaflet margins	distributed along the entire leaflet margins	restricted to revolute area of leaflet margin
Trichomes in midvein on the abaxial surface	present	present	Absent
Trichomes on lamina	present	absent	Absent
Number of secondary veins	8–12	10–15	17–23
Secondary venation relief	flat	prominulous	prominulous
Intersecondary venation relief	flat	flat	prominulous
Petal length	to 3 mm long	to 3 mm long	to 2 mm long
Fruit shape	globose to obovoid	pyriform to obovoid	oblong, fusiform, ellipsoidal, pyriform
Styles developing into protuberances in the fruit	absent	present	Absent
Lenticels in fruit surface	absent	small lenticels	large lenticels
Endocarp in cross-section	oblong	elliptical to round	round
Fibrous matrix	soft and spongy, little fibrous	soft and spongy, little fibrous	hard and very fibrous
Endocarp surface after fibrous matrix removal	smooth	shallowly ridged	prominently crested
Spiny projections of endocarp	absent	short	long
Ridges of endocarp	absent	unconnected	connected
Size of the fenestrae covering the opercula	one much larger than remainder	one or two larger than remainder	one to three larger than remainder

surface, and flexuous trichomes occurring along the margin, in the petiolules, and along the midrib abaxially; the leaflet lamina is otherwise glabrous (Figure 8A). Leaflets of *S. tuberosa* are essentially flat, with trichomes occurring in the petiolules, midrib, along the margins, and also in both the adaxial and abaxial surfaces of lamina, some individuals bearing densely pubescent leaflets (Figure 8B). Leaflets of *S. venulosa* have margins at base distinctly revolute towards the abaxial surface, with a tuft of flexuous trichomes to 0.6mm long usually restricted to the revolute area but sometimes also occurring in the petiolules; the leaflet lamina is otherwise glabrous (Figure 8C).

Flowers of *umbu-cajá*, *S. tuberosa* and *S. venulosa* are essentially identical, with the

only difference that *S. venulosa* has smaller petals, up to 2 mm in *S. venulosa* versus up to 3 mm in the other species (Figure 9). There is some overlap in the shape of fruits from *umbu-cajá*, *S. tuberosa* and *S. venulosa*, but generally fruits can also be useful to distinguish between the three taxa. Fruits of *umbu-cajá* are pyriform to obovoid (Figures 10B, 11), those of *S. tuberosa* are globose to obovoid (Figure 10A), and fruits of *S. venulosa* are the most variable, ranging from fusiform to oblong, ellipsoidal or pyriform (Figure 10C). Fruits of *S. tuberosa* lack lenticels, which are present in the exocarp of both *umbu-cajá* and *S. venulosa*, with lenticels being more prominent in the latter. Fruits of *umbu-cajá* and *S. tuberosa* have thick and juicy mesocarps, whereas *S. venulosa* has fruits with

scant mesocarp. There are also differences in smell and taste of all three taxa, although comparative studies of volatile and other compounds have not yet been carried out.

The endocarps of *umbu-cajá*, *S. tuberosa* and *S. venulosa* are enclosed within a fibrous matrix, but this matrix is much less fibrous in *umbu-cajá* and *S. tuberosa*. The fibrous matrix surrounds a layer of soft spongy tissue, and this tissue encloses the woody endocarp. The morphology of the endocarp can be observed after the fibrous matrix and subtending spongy tissue are removed with the aid of a wire brush. Endocarps of *umbu-cajá* are elliptical to round in cross-section, with unconnected shallow ridges running lengthwise, and short spiny projections in the proximal and distal ends of the endocarp which do not cover the opercula in the distal end; the endocarps have four to five opercula, with one or two larger than the remainder and containing viable seeds (Figures 12, 13). Endocarps of *S. tuberosa* are laterally compressed (oblong in cross-section) and have a smooth surface, lacking projections in the distal and proximal ends; the endocarps have five opercula, one or two of them being much enlarged and containing a viable seed (Figure 12). Endocarps of *S. venulosa* are round in cross-section, with many prominent ridges or crests running lengthwise which are usually connected with each other; spiny projections occur in both the proximal and distal ends of the endocarp, the projections in the distal end usually covering the opercula; the endocarps have four to five opercula, with two or three of these being larger than the remainder and containing viable seeds (Figure 12). Although endocarps of *umbu-cajá* vary somewhat (Figure 13), the endocarps of *umbu-cajá*, *S. tuberosa* and *S. venulosa* are sufficiently different to enable the taxonomic recognition of each as distinct species based on endocarp morphology alone.

The shallowly-crested endocarps of *umbu-cajá* seem morphologically intermediate between the smooth endocarps of *S. tuberosa* and the prominently-ridged endocarp of *S. venulosa*, and

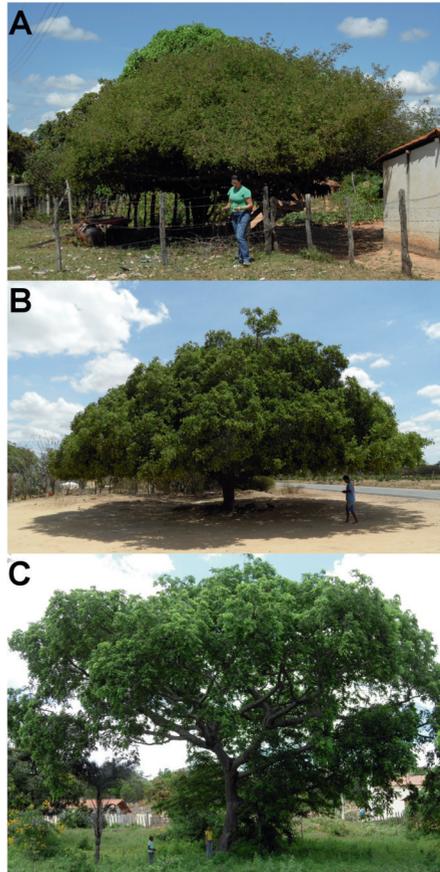


Figure 7. Comparison of tree architecture of *Spondias tuberosa*, the new species *S. bahiensis* (*umbu-cajá*), and *S. venulosa*.

A. *Spondias tuberosa*, notice dense branching and umbrella-shaped canopy; **B.** *Spondias bahiensis* (*umbu-cajá*), with less dense branching and also umbrella-shaped canopy; **C.** *Spondias venulosa*, with less dense branching and funnelliform canopy. A person next to each of the trees provides scale. Photographs by Marlon Machado.

could be interpreted as a result of hybridization between *S. tuberosa* and *S. venulosa* giving rise to the intermediate features of *umbu-cajá* endocarps. Another possible explanation for the observed differences in endocarp ornamentation, that not necessarily denies the hybrid origin

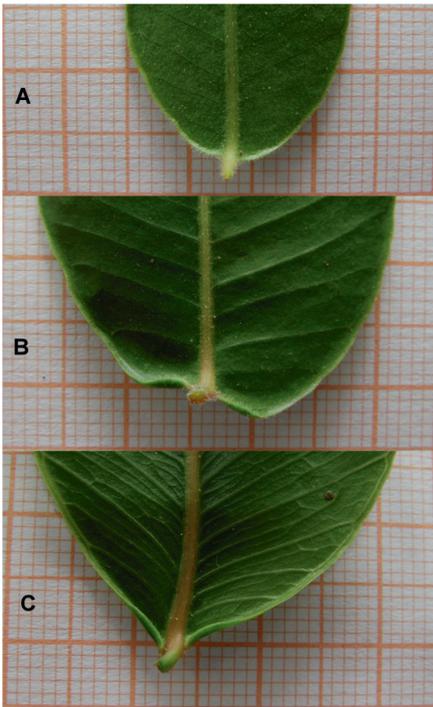


Figure 8. Comparison of leaflet morphology of *Spondias tuberosa*, the new species *S. bahiensis* (*umbu-cajá*), and *S. venulosa*.

A. *Spondias tuberosa*, abaxial view of basal portion of leaflet displaying flat margins, with trichomes scattered over all structures; secondary venation flat, hardly noticeable; **B.** *Spondias bahiensis*, abaxial view of basal portion of leaflet displaying slightly revolute margins, with trichomes restricted to the revolute area, margins of leaflet, petiolule and midvein; secondary venation prominulous, tertiary venation flat, hardly noticeable; **C.** *Spondias venulosa*, abaxial view of basal portion of leaflet displaying revolute margins, with trichomes restricted to the revolute area; secondary and tertiary venation prominulous. A. Feira de Santana, Bahia, M.C.Machado 1282; B. Feira de Santana, Bahia, M.C.Machado 1280; C. Feira de Santana, Bahia, M.C.Machado 1283. Photographs by Marlon Machado.

hypothesis, is a developmental one: both *umbu-cajá* and *S. tuberosa* bear ripe fruits two to three months after flowering, whereas fruits of *S. venulosa* take eight to ten months to mature (Machado, pers. obs.). It is possible that the longer period of fruit development in *S. venulosa* be related to the increased lignification and elaborated surface ornamentation of the endocarp in this species, whereas in *umbu-cajá* and *S. tuberosa* the shorter period of fruit development impede a very elaborated surface ornamentation to be created. The crests in the endocarps of both *umbu-cajá* and *S. venulosa* might indeed be a good synapomorphy of the close phylogenetic relationship between these taxa.

CONCLUSIONS

Multiple lines of evidence (morphological, morphometric, genetic) suggest that *umbu-cajá* is indeed a hybrid as often stated in the literature, though not between *Spondias mombin* and *S. tuberosa* but rather between the latter and *S. venulosa*. *Umbu-cajá* displays morphological intermediacy between *S. tuberosa* and *S. venulosa*, and there is well-supported phylogenetic incongruence in the placement of *umbu-cajá* between the nuclear ETS and the plastid cpDNA datasets, with *umbu-cajá* resolved as closest to *S. venulosa* in the cpDNA dataset and closest to *S. tuberosa* in the ETS dataset, indicating that *umbu-cajá* might have a hybrid origin with *S. venulosa* and *S. tuberosa* as its parents. However, *umbu-cajá* was found to have diverged from *S. venulosa* 3.79 million years ago, indicating that this taxon originated from natural processes.

Umbu-cajá appears to be a domesticated taxon which remained undescribed precisely due to its putative hybrid origin, because wild populations are unknown, and also due to a relative scarcity of herbarium collections — not because of its rarity, but rather because common and cultivated plants are seldom collected and thus are often under-represented

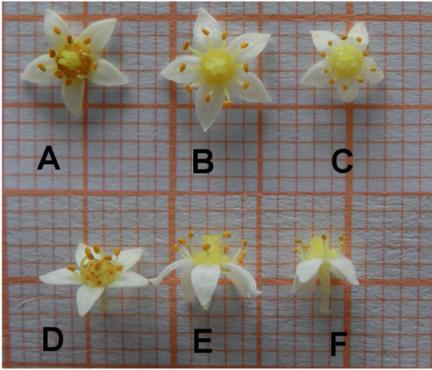


Figure 9. Comparison of flowers of *Spondias tuberosa*, the new species *S. bahiensis* (*umbu-cajá*), and *S. venulosa*. **A, D.** Top and side views of *Spondias tuberosa* flower, petals are patent at anthesis; **B, E.** Top and side views of *S. bahiensis* flower, petals are reflexed at anthesis; **C, F.** Top and side views of *S. venulosa* flower, petals are reflexed at anthesis. Dimensions of *S. venulosa* flowers are smaller than in the preceding species, but mostly because *S. venulosa* has shorter petals; other characteristics are very similar. Notice the cucullated apex of petals in all species. A, D. Feira de Santana, Bahia, M.C.Machado 1282; B, E. Feira de Santana, Bahia, M.C.Machado 1280; C, F. Feira de Santana, Bahia, M.C.Machado 1283. Photographs by Marlon Machado.

in herbaria (ter Steege et al. 2011). In spite of the overall high morphological similarity between *umbu-cajá*, *S. tuberosa* and *S. venulosa*, there are many features that distinguish and allow easy identification of all three taxa.

Umbu-cajá is a truly a domesticated crop: so far it is only known from cultivation, a situation also found elsewhere in the genus (e.g. *Spondias dulcis*), as well as in other plant species (e.g. *Calendula officinalis* L. (Heyn et al. 1975), *Flacourtia jangomas* (Loureiro) Raeuschel (Sleumer 1954), *Ginkgo biloba* L. (Shen et al. 2004), *Pachira glabra* Pasq. (Robyns 1960)), where unequivocal wild populations and precise natural distributions are unknown or only tentatively determined. *Umbu-cajá* has a number of features of the domestication syndrome, such as larger, juicier, less acid, and quicker maturing fruits

(Figures 10, 11), and vegetative propagation of superior clones. It is possible that *umbu-cajá* originated from small, localized populations that evolved features rendering it attractive to man; subsequently, widespread cultivation coupled with the clearing of original vegetation has obscured the origins of *umbu-cajá*, which nowadays is found solely in cultivation as a domesticated taxon.

Here we follow the opinion of Knapp et al. (2013) in that domesticated taxa should be designated as distinct species, even if their wild progenitors are known, because selection pressures in cultivation are distinct from natural selection pressures occurring in the wild, conferring domesticated plants a different evolutionary path than that of their wild counterparts. Formal recognition of the Bahian *umbu-cajá* also serves a practical purpose. Since the vernacular name *umbu-cajá* has been applied to more than one taxon, there is a clear confusion in the literature, with authors often comparing results of studies carried out on different taxa. Formally recognizing the Bahian *umbu-cajá* as a distinct species will hopefully help to resolve the ambiguities found in the literature and aid in the communication about this taxon — one of the primary goals of taxonomy. We therefore describe the Bahian *umbu-cajá* as a new species, as follows:

Spondias bahiensis P.Carvalho, Van den Berg & M.Machado, sp. nov. (Figures 7B, 8B, 9B, 9E, 10B, 11, 12B, 13 and 14)

Haec species S. tuberosae affinis, sed differt statura (4–8 m vs. 3–5m alta), ordinatione ramificationis (arbor vertice aspectu apertiore vs. aspectu clausiore et ramis tortuosis), margine foliolorum ad basim abaxialiter curvata (vs. plana), trichomatibus in lamina foliolorum absentibus (conspicuis in S. tuberosa), numero venarum secundariarum (10–15 vs. 8–12), venis secundariis prominulis (vs. planis), stylis in fructu protuberationem evolutis, superficie fructus cum lenticellis, superficie endocarpi leviter cristata (vs. laeve), endocarpo

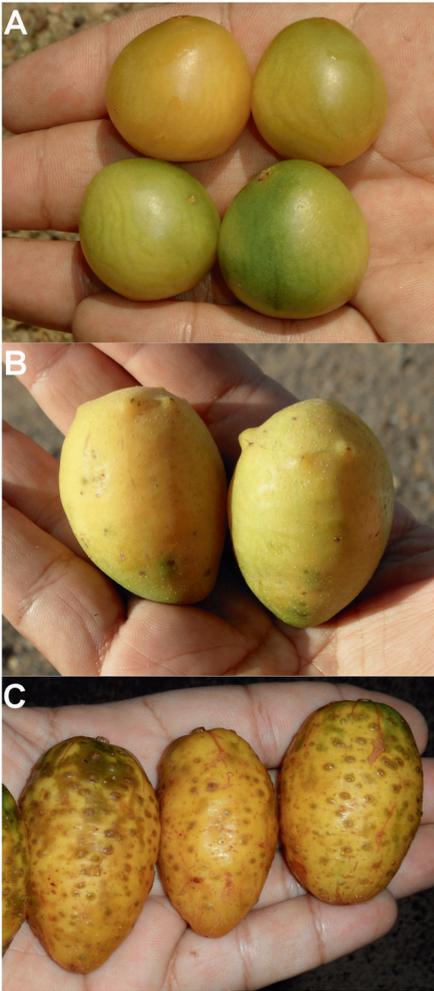


Figure 10. Comparison of fruits of *Spondias tuberosa*, the new species *S. bahiensis* (*umbucajá*), and *S. venulosa*.

A. Fruits of *Spondias tuberosa*, round and without lenticels; **B.** Fruits of *Spondias bahiensis*, oblong, with small lenticels scattered through the surface of fruit, and conical protuberances on distal end resulting from the development of the styles; **C.** Fruits of *Spondias venulosa*, ellipsoidal, with large lenticels in the surface of fruit. A. Bahia, Paulo Afonso, M.C.Machado, M.O.T.Menezes & F.R.Paiva 1482; B. Bahia, Iraquara, M.C.Machado, F.M.Ferreira & T.T.S.Silva 1367; C. Rio de Janeiro, São Pedro da Aldeia, M.C.Machado & N.G.Antas 1570. Photographs by Marlon Machado.

in sectione transversali elliptico usque rotundo (vs. oblongo) cum projecturis spineis extremitatibus distali et proximali. *S. bahiensis* quoque *S. venulosae* affinis, sed differt statura (4–8 m vs. 6–20m alta), arbore vertice umbellato (vs. infundibuliformi), superficie abaxiali foliolorum in marginem et costam cum trichomatibus (vs. glabra), numero venarum secundariorum (10–15 vs. 17–23), venis intersecondariis planis (vs. prominulis), petalis longioribus (usque 3mm vs. 2mm), stylis in fructu protuberantem evolutis, lenticellis fructuum parvis (vs. magnis), superficie endocarpi leviter cristata (vs. prominenter cristata), cristis endocarpi interruptis (vs. ininterruptis), matrice endocarpi amplexentis vix fibrosa suavi spongiosaque (vs. rigida et fibrosa), projecturis spineis extremitatibus distali et proximali endocarpi brevibus fenestras non obtegentibus (vs. longis et fenestras obtegentibus).

A new species, similar to *Spondias tuberosa* Arruda, from which it differs in stature (4–8 m in *S. bahiensis* versus 3–5m in height in *S. tuberosa*), branching pattern (more open canopy versus dense, crooked branching pattern), leaflet margin at base (curved towards abaxial surface versus flat), trichomes in leaflet lamina (absent versus present), number of secondary veins (10–15 pairs versus 8–12 pairs) secondary venation relief at abaxial surface (prominulous versus flat), styles developing into protuberances in the fruit (present versus absent), lenticels on fruit surface (present versus absent), endocarp surface (shallowly ridged versus smooth), endocarp shape in cross-section (elliptical to round versus oblong), and spiny projections at both the distal and proximal ends of endocarp (present versus absent). *Spondias bahiensis* is also similar to *Spondias venulosa* (Engl.) Engl., from which it differs in stature (4–8 m in *S. bahiensis* versus 6–20m in height in *S. venulosa*), canopy shape (umbrella-shaped versus funnellform), trichomes on leaflet margin and on midvein at abaxial surface (present



Figure 11. Typical fruits of *umbu-cajá*, *Spondias bahiensis* (specimen M.C.Machado 1279, Feira de Santana, Bahia), pyriform in shape and with the distal region of the fruit displaying protuberances derived from the enlargement of styles. Photograph by Marlon Machado.

versus absent), number of secondary veins (10–15 pairs versus 17–23 pairs) intersecondary venation relief at abaxial surface (flat versus prominulous), petal length (3 mm long versus 2 mm long), styles developing into protuberances in the fruit (present versus absent), lenticels on fruit surface (small versus large), endocarp surface (shallowly ridged versus prominently crested), ridges of endocarp (unconnected versus connected), fibrous matrix surrounding endocarp (soft and spongy, scanty fibrous versus hard and very fibrous), and spiny projections at both the distal and proximal ends of endocarp (short, not covering the fenestrae versus long, covering the fenestrae).

Type:—BRAZIL. Bahia: Iaçú, Povoado de Lajedo Alto, 12°43'31.3"S, 39°52' 25.2"W, 258m, 5 December 2010, *C. van den Berg, D.Nascimento & P.L.R. Moraes* 1974 (Holotype: HUEFS 145099; Isotypes: CEPEC, HUEFS, ALCB, HRB, SP, RB, CEN, MBM, INPA,

K, MO, NY, P, IPA, MEXU).

Trees 4–8 m tall, with an umbrella-shaped canopy, usually evergreen but becoming deciduous when growing in drier areas; trunk usually single, short, 1–2 m in height and up to 40 cm diam.; outer bark gray, relatively thin, with vertical stripes of raised lenticels; branches somewhat succulent, young branches with thickened green tips, gradually becoming grayish as they age. Leaves (8)10–24(27) cm long, imparipinnate, 2–4(5)-jugate; petiole 5–7 cm long \times 1.5–2 mm diam, base pulvinate, pulvinus 4–5 \times 3–3.5 mm, petiole and rachis pilose, trichomes 0.4–0.6 mm long; lateral petiolules 1.5–3 mm long, the terminal one 5–15 mm long, pilose, trichomes 0.4–0.6 mm long; leaflets 3–7 \times 1.5–4.5 cm, (sub)opposite, ovate, 1.2–2.4 \times longer than wide, lamina chartaceous, glabrous, apex acuminate, the acumen 1–7 \times 1–5 mm, triangular,

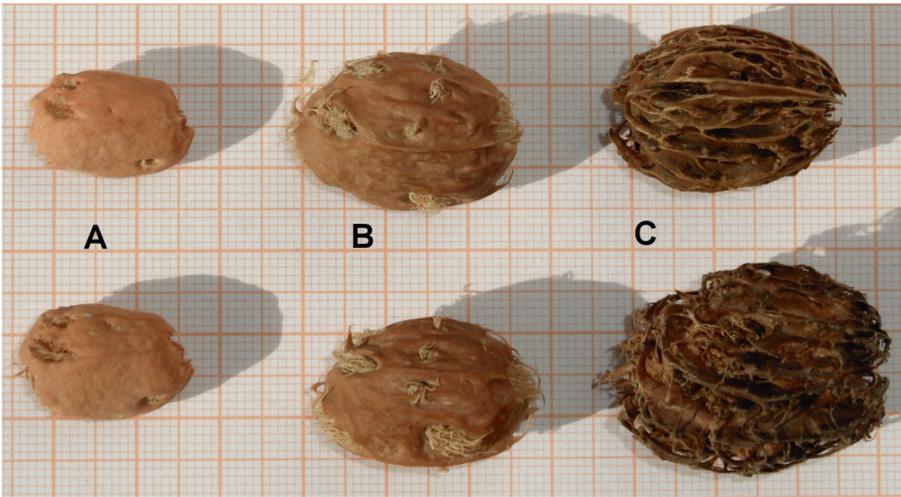


Figure 12. Comparison of endocarps of *Spondias tuberosa*, the new species *S. bahiensis* (*umbu-cajá*), and *S. venulosa*. **A.** Endocarps of *Spondias tuberosa*, the surface smooth and without ridges or projections; **B.** Endocarps of *Spondias bahiensis*, the surface with shallow unconnected ridges and short spiny projections in the distal and proximal ends; **C.** Endocarps of *Spondias venulosa*, the surface displaying many raised, connected crests, and spiny projections in the distal and proximal ends. A. Feira de Santana, Bahia, M.C.Machado 1282; B. Feira de Santana, Bahia, M.C.Machado 1275; C. (upper) Feira de Santana, Bahia, M.C.Machado 1283; C. (lower) Nova Itarana, Bahia, M.C.Machado, F.M.Ferreira & T.T.S.Silva 1253. Photograph by Marlon Machado.

1–2 × longer than wide, tapering to an acute tip, base symmetrical to slightly asymmetrical, margins curved towards abaxial surface, the curved area pilose, trichomes 0.4–0.6 mm long, margins entire, with trichomes 0.4–0.6 mm long, midvein prominent on abaxial surface with trichomes 0.4–0.6 mm long, prominulous and glabrous on adaxial surface, secondary veins 10–15 pairs, glabrous, brochidodromous, straight or slightly arcuate, acute to the midvein, spacing decreasing toward the base, angle increasing toward the base, flat at the adaxial surface, prominulous at the abaxial surface, intramarginal vein present, intersecondary veins parallel to secondaries, intercostal tertiary vein fabric admedially ramified, quaternary vein fabric freely ramifying. Inflorescences thyriform, 10–15 cm long, secondary axes to 5 cm, the axes greenish, densely pilose, trichomes 0.4–0.6 mm long; bracts subtending secondary axes 6–8 mm long, narrowly lanceolate, membranaceous, and

caducous; bracteoles 2–4 mm long, narrowly lanceolate; pedicel to 2.5 mm long, to 0.3 mm from base to articulation point, cylindrical, pilose, trichomes 0.4–0.6 mm long. Buds subglobose. Flowers 5-merous, ca. 2 mm long at anthesis; calyx 1.5–2 mm overall, slightly shorter than the disk, patent, lobes 0.4–0.6 mm long, triangular, glabrous; petals 3 × 1.2 mm, ovate, patent to reflexed at anthesis, glabrous on both surfaces, apex acute, cucullated; androecium pentadynamous and the same length as the pistil, stamens 10, antesealous stamens to 1.8 mm long, antepetalous stamens to 1.6 mm long, filaments cylindrical, broader at base and tapering towards anther, anthers to 5 mm long, oblong, dorsifixed; disk 0.5 × 2 mm, decalobate, surface densely papillose; pistil well-developed at anthesis, to 1.8 × 0.8 mm, basally syncarpous, carpels 5, the five styles to 1.3 mm long, papillose, slightly divergent, capped by slightly oblique, compressed-ovoid

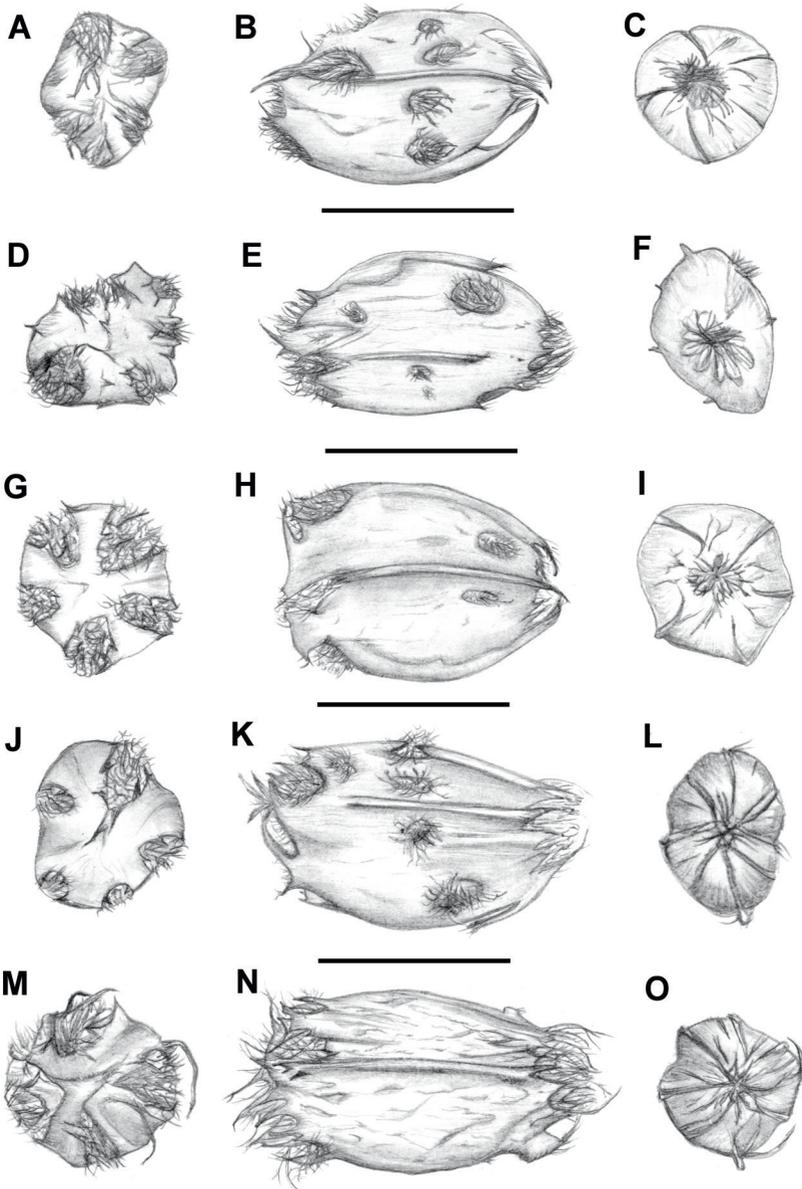


Figure 13. Variation in endocarps of the new species *Spondias bahiensis* (*umbu-cajá*). **A, D, G, J, M.** Distal view, displaying the five fenestrae containing the opercula; **B, E, H, K, N.** Side view, displaying the longitudinal ridges of the endocarp, and the presence of further fenestrae; **C, F, I, L, O.** Proximal view. A-C. Feira de Santana, Bahia, *M.C.Machado* 1275; D-F. Morro do Chapéu, Bahia, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1399; G-H. Itiúba, Bahia, *M.C.Machado, M.O.T.Menezes & F.R.Paiva* 1467; J-L. Planaltino, Bahia, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1335; M-O. Vitória da Conquista, Bahia, *M.C.Machado, M.O.T.Menezes & F.R.Paiva* 1447. Drawings by Pétala Gomes Ribeiro.

stigmas. Fruit a pyriform to obovoid drupe, (4)4.8–5.5 × 2.5–3.2 cm, pale to golden yellow when ripe, remnants of the styles visible as conical protuberances on distal tip; exocarp thin, smooth, the surface covered with small lenticels; mesocarp juicy; fibrous matrix covering the endocarp present, weak, spongy, quickly decaying to reveal the bony endocarp after fruit dispersion; endocarp 2–3 × 1.5–2 cm, elliptical to round in cross-section, 4–5-locular (one or two fertile), distal end with four to five bipartite opercula, the opercula located within individual fenestra and covered by fibrous tissue, fenestrae corresponding to the fertile locule(s) noticeably larger than the remainder, margin of apical fenestrae with short spiny projections, the spiny projections not covering the opercula, proximal end with short spiny projections, endocarp surface relatively smooth, with 4–5 shallow ridges running the length of the endocarp from the apical opercula fenestrae towards the proximal end, the ridges ending in spiny projections, varying numbers of fenestrae also present near the proximal end of the endocarp, these fenestrae absent in some collections. Seedlings with linear cotyledons to 3 cm long; radicle swelling and developing into a tuberous storage taproot; eophylls trifoliolate, leaflets ovate, margin serrate.

Additional Collections (paratypes):— BRAZIL. ALAGOAS: Igaci, 09°32'44.3"S, 36°39'07.8"W, 301m, 30 Mar 2013, *M.C. Machado, M.O.T.Menezes & F.R.Paiva 1488* (HUEFS). BAHIA: Without locality, 12 Sep 1940, *I.Menezes 10* (RB); Alagoinhas, Rua Juracy Magalhães, bairro Centro, 14 Sep 2000, *L.E.Figueroa 55* (HUEFS); Andaraí, 12°28'29.4"S, 41°03'26.6"W, 543m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1364* (HUEFS); Antônio Cardoso, 12°24'16.8"S, 39°10'27.5"W, 139m, 8 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva 1320* (HUEFS); Antônio Gonçalves, 10°35'26.0"S, 40°16'28.5"W, 481m, 26 Mar 2013, *M.C. Machado, M.O.T.Menezes & F.R.Paiva 1462* (HUEFS); Baixa Grande, 11°57'32.3"S, 40°11'02.6"W, 384m, 11 Feb 2013, *M.C. Machado,*

F.M.Ferreira & T.T.S.Silva 1403 (HUEFS); Baixa Grande, 12°00'05.1"S, 40°05'18.3"W, 346m, 11 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1404* (HUEFS); Banzaê, Povoado de Marcação, Área indígena Kiriri, fazenda Picos, 10°37'08"S, 38°36'09"W, 380m, 21 Sep 2002, *C.Correia, L.M.Pacheco & Índios Kiriri 161* (HUEFS); Boa Vista do Tupim, 12°27'06.7"S, 40°37'56.4"W, 548m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1359* (HUEFS); Brejões, 13°03'42.0"S, 39°57'24.1"W, 849m, 23 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1441* (HUEFS); Cachoeira, Riacho Congu. Vale dos Rios Paraguaçu e Jacuípe, Nov 1980, *Grupo Pedra do Cavalo 942* (CEPEC, HUEFS); Candeal, 8 km al N de Tanquinho, camino a Ichu, 15 Jan 1997, *M.M.Arbo, J.G.Jardim, M.S.Ferruci & S.C. Sant'Ana 7239* (CEPEC, K, MO, NY, SPF); Conceição do Coité, 11°35'14.8"S, 39°12'02.9"W, 374m, 27 Mar 2013, *M.C. Machado, M.O.T.Menezes & F.R.Paiva 1474* (HUEFS); Cruz das Almas, B97, entre Cruz das Almas e Sapeaçu, prox. das vendas de suco de laranja, 12°42'28"S, 39°09'42"W, 260m, 5 Dec 2010, *C. van den Berg, D.Nascimento & P.L.R.Moraes 1978* (HUEFS); Cruz das Almas, 12°40'20.9"S, 39°05'55.3"W, 208m, 24 Feb 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1406* (HUEFS); Feira de Santana, Bairro Pampalona, Rua Joana Pereira da Silva, 411, 2 Jul 2002, *S.Santos 42* (HUEFS); Feira de Santana, Campus UEFS, 6 Jan 2009, *C. Chamusca 11* (HUEFS); Feira de Santana, 12°00'05.4"S, 39°10'35.3"W, 187m, 12 Aug 2012, *M.C.Machado, C. van den Berg, C.R. Buzatto & A.Sanguinetti 1268* (HUEFS); Feira de Santana, 12°12'06.2"S, 38°58'33.5"W, 237m, 21 Aug 2012, *M.C.Machado 1273* (HUEFS); Feira de Santana, 12°12'06.2"S, 38°58'33.5"W, 237m, 21 Aug 2012, *M.C.Machado 1274* (HUEFS); Feira de Santana, 12°12'06.3"S, 38°58'33.2"W, 239m, 21 Aug 2012, *M.C.Machado 1275* (HUEFS); Feira de Santana, 12°12'07.4"S, 38°58'33.6"W, 237m, 21 Aug 2012, *M.C. Machado 1276* (HUEFS); Feira de Santana, 12°12'05.9"S, 38°58'25.5"W, 251m, 21 Aug 2012, *M.C.Machado 1279* (HUEFS); Feira

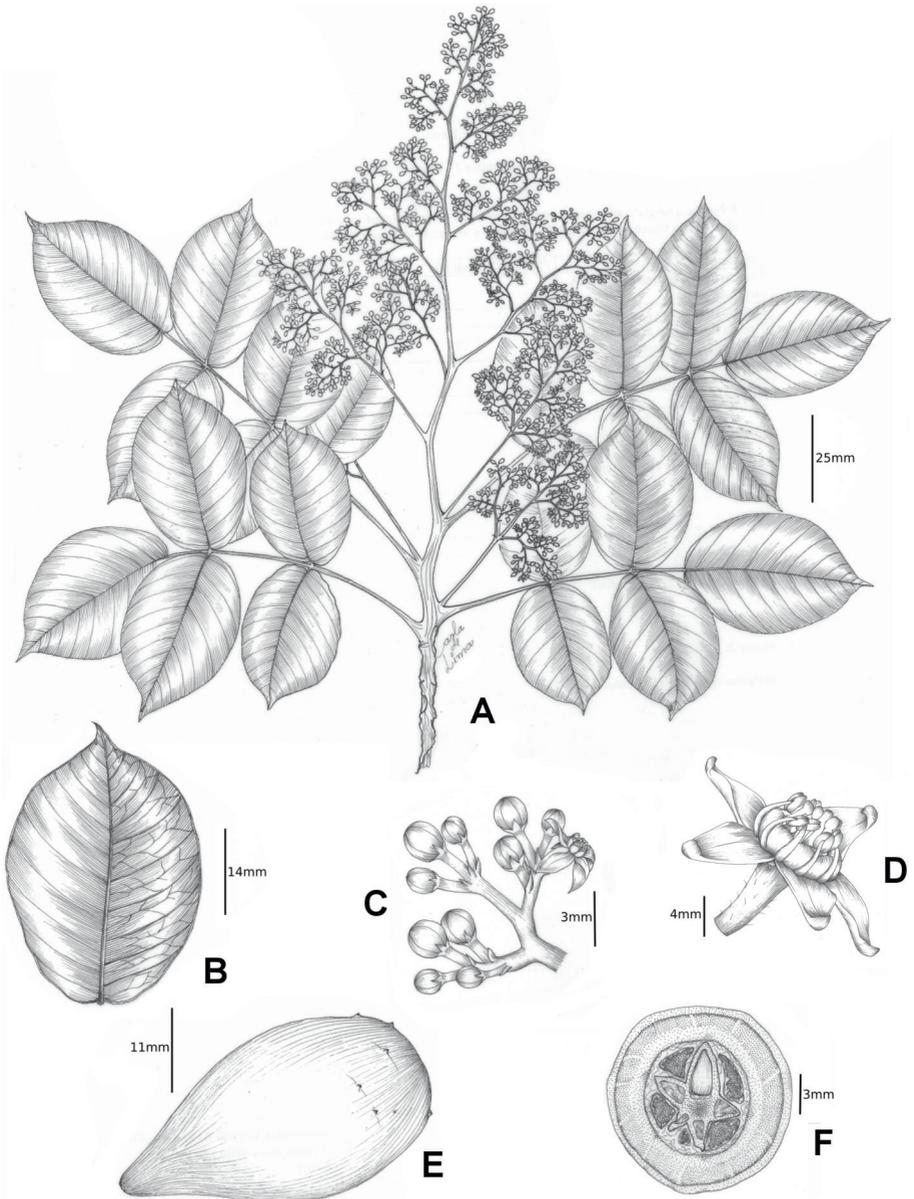


Figure 14. *Spondias bahiensis* P.Carvalho, Van den Berg & M.Machado.

A. Leafy branch with inflorescence. **B.** Leaflet. **C.** Inflorescence with floral buds and flower. **D.** Flower. **E.** Fruit. **F.** Cross-section of fruit showing position of endocarp, the upper locule with a fertile seed. Drawings by Carla de Lima.

- de Santana, 12°12'03.6"S, 38°58'25.1"W, 246m, 21 Aug 2012, *M.C.Machado 1280* (HUEFS); Feira de Santana, 12°11'58.5"S, 38°58'07.7"W, 245m, 21 Aug 2012, *M.C.Machado 1285* (HUEFS); Feira de Santana, Feira VI, 12°12'18.6"S, 38°58'02.6"W, 246m, 21 Aug 2012, *M.C.Machado 1286* (HUEFS); Feira de Santana, Feira VI, 12°12'18.0"S, 38°58'07.6"W, 246m, 21 Aug 2012, *M.C.Machado 1287* (HUEFS); Feira de Santana, 12°12'07.4"S, 38°58'33.6"W, 237m, 25 Jan 2013, *M.C.Machado 1314* (HUEFS); Feira de Santana, entrada do bairro Papagaio, 12°12'28.6"S, 38°57'54.4"W, 200m, 25 Jan 2013, *M.C.Machado 1315* (HUEFS); Feira de Santana, 12°11'53.7"S, 38°58'08.2"W, 245m, 25 Jan 2013, *M.C.Machado 1316* (HUEFS); Feira de Santana, Fazenda Chapada, 12°15'06.7"S, 39°05'42.6"W, 205m, 26 Jan 2013, *E.Melo, M.C.Machado & B.M.Silva 11931* (HUEFS); Feira de Santana, 12°17'48.7"S, 39°00'41.8"W, 156m, 26 Jan 2013, *E.Melo, M.C.Machado & B.M.Silva 11933* (HUEFS); Feira de Santana, 12°11'54.2"S, 38°58'08.2"W, 235m, 30 Jan 2013, *M.C.Machado 1317* (HUEFS); Feira de Santana, 12°14'07.1"S, 39°04'11.5"W, 193m, 2 Feb 2013, *E.Melo, M.C.Machado & B.M.Silva 11943* (HUEFS); Feira de Santana, 12°14'32.8"S, 39°04'30.4"W, 184m, 2 Feb 2013, *E.Melo, M.C.Machado & B.M.Silva 11944* (HUEFS); Feira de Santana, 12°15'42.4"S, 39°03'57.5"W, 195m, 2 Feb 2013, *E.Melo, M.C.Machado & B.M.Silva 11946* (HUEFS); Iaçú, Dentro da Vila de Lajedo Alto, 12°43'31"S, 39°52'25"W, 258m, 5 Dec 2010, *C. van den Berg, D.Nascimento & P.L.R.Moraes 1977* (HUEFS); Iaçú, Lajedo Alto, 12°43'34.7"S, 39°52'23.1"W, 278m, 15 Oct 2012, *D.Cardoso & M.C.Machado 3265* (HUEFS); Ipirá, 12°20'03.5"S, 39°56'56.8"W, 292m, 25 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1455* (HUEFS); Iramaia, 13°36'54.6"S, 40°48'04.4"W, 388m, 24 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1450* (HUEFS); Iraquara, 12°11'55.0"S, 41°36'54.7"W, 761m, 18 Apr 2011, *M.C.Machado & J.G.Carvalho-Sobrinho 1261* (HUEFS); Iraquara, 12°12'25.2"S, 41°32'45.0"W, 729m, 18 Apr 2011, *M.C.Machado & J.G.Carvalho-Sobrinho 1262* (HUEFS); Iraquara, 12°09'39.7"S, 41°26'36.3"W, 878m, 18 Apr 2011, *M.C.Machado & J.G.Carvalho-Sobrinho 1263* (HUEFS); Iraquara, 12°21'27.5"S, 41°36'30.5"W, 724m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1367* (HUEFS); Iraquara, 12°21'25.8"S, 41°36'28.2"W, 725m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1368* (HUEFS); Iraquara, 12°15'40.4"S, 41°33'48.4"W, 721m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1372* (HUEFS); Iraquara, 12°16'15.5"S, 41°30'26.6"W, 700m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1374* (HUEFS); Iraquara, 12°17'09.6"S, 41°30'48.2"W, 672m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1376* (HUEFS); Iraquara, 12°20'52.3"S, 41°32'29.0"W, 662m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1379* (HUEFS); Iraquara, 12°14'15.8"S, 41°35'29.7"W, 718m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1383* (HUEFS); Iraquara, 12°14'01.4"S, 41°34'45.2"W, 718m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1384* (HUEFS); Iraquara, 12°13'28.9"S, 41°30'07.4"W, 702m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1386* (HUEFS); Iraquara, 12°12'35.3"S, 41°26'34.4"W, 988m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1387* (HUEFS); Iraquara, 12°09'39.7"S, 41°26'36.3"W, 878m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1389* (HUEFS); Iraquara, 12°12'25.2"S, 41°32'45.0"W, 729m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1392* (HUEFS); Iraquara, 12°11'55.0"S, 41°36'54.7"W, 761m, 10 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1394* (HUEFS); Itaberaba, 12°31'31.7"S, 40°17'40.1"W, 260m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1336* (HUEFS); Itaberaba, 12°31'31.7"S, 40°17'40.1"W, 260m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1337* (HUEFS); Itaberaba, 12°30'32.7"S, 40°15'43.2"W, 270m, 25 Mar 2013, *M.C.Machado, M.O.T.Menezes*

& *F.R.Paiva 1453* (HUEFS); Itaberaba, 12° 26'37.9"S, 40°07'00.0"W, 294m, 25 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1454* (HUEFS); Itabuna, Próximo ao escritório local da CEPLAC, 3 Mar 1998, *A.M.Carvalho & C.Kersul 1701* (CEPEC); Itapetinga, 15°14'28.1"S, 40°14'23.1"W, 297m, 14 Oct 2012, *D.Cardoso & M.C.Machado 3258* (HUEFS); Itatim, 12°40'23.7"S, 39°39' 25.2"W, 219m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1324* (HUEFS); Itatim, 12°40'24.1"S, 39°39'25.3"W, 220m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1325* (HUEFS); Itiúba, 10°42' 13.9"S, 39°56'19.3"W, 384m, 26 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1464* (HUEFS); Itiúba, 10°42'21.6"S, 39°57' 45.2"W, 408m, 26 Mar 2013, *M.C. Machado, M.O.T.Menezes & F.R.Paiva 1465* (HUEFS); Itiúba, 10°42'23.8"S, 39°58'30.8"W, 414m, 26 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1467* (HUEFS); Itiúba, 10°42' 39.4"S, 40°01'23.0"W, 413m, 26 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1468* (HUEFS); Jacobina, Catinga do Moura, 11°04'08.7"S, 40°45'13.4"W, 753m, 25 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1458* (HUEFS); Lajedinho, 12°26' 22.2"S, 40°50'03.8"W, 600m, 12 Oct 2012, *D.Cardoso & M.C.Machado 3250* (HUEFS); Lajedinho, 12°26'43.2"S, 40°43'05.9"W, 574m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1360* (HUEFS); Lajedinho, 12° 26'43.6"S, 40°43'50.5"W, 562m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1361* (HUEFS); Lajedinho, 12°26'22.2"S, 40°50'03.8"W, 600m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva 1362* (HUEFS); Lajedinho, 12°26'22.2"S, 40°50' 03.8"W, 600m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva 1363* (HUEFS); Lençóis, 12°30'21.1"S, 41°12'35.0"W, 380m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1365* (HUEFS); Lençóis, 12° 30'21.0"S, 41°12'38.0"W, 376m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1366* (HUEFS); Maracás, Fazenda Tanquinho, ramal com entrada no km 23 da rodovia

Maracás/Planaltino, lado esquerdo. Sede da Fazenda a 2 km da entrada, 3 Mar 1988, *L.A.Mattos-Silva 2299* (CEPEC, K, NY); Maracás, Fazenda Tanquinho, ramal com entrada no km 23 da rodovia Maracás/ Planaltino, lado esquerdo. Sede da Fazenda a 2 km da entrada, 3 Mar 1988, *L.A.Mattos-Silva 2301* (CEPEC, HUEFS, K, MBM, NY); Maracás, 13°30'12.5"S, 40°33'27.9"W, 772m, 24 Mar 2013, *M.C.Machado, M.O.T. Menezes & F.R.Paiva 1451* (HUEFS); Morro do Chapéu, Ventura, 11°41'28.1"S, 40°51'14.2"W, 791m, 11 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1398* (HUEFS); Morro do Chapéu, Ventura, 11°41'28.0"S, 40°51' 13.2"W, 791m, 11 Feb 2013, *M.C.Machado, F.M. Ferreira & T.T.S.Silva 1399* (HUEFS); Mundo Novo, Fazenda Jequitibá, 12°02'W, 40°29'S, 604m, 24 Nov 2006, *P.A.Melo 139* (HUEFS); Nova Fátima, 11°33'34.7"S, 39°40'50.7"W, 294m, 26 Mar 2013, *M.C.Machado, M.O.T. Menezes & F.R.Paiva 1470* (HUEFS); Nova Itarana, 13°05'27.7"S, 40°08'21.2"W, 769m, 15 Oct 2012, *M.C.Machado & D.Cardoso 1293* (HUEFS); Pindobaçu, 10°39'05.5"S, 40°18' 23.4"W, 513m, 26 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva 1459* (HUEFS); Pindobaçu, 10°37'10.9"S, 40°17'20.3"W, 457m, 26 Mar 2013, *M.C.Machado, M.O.T. Menezes & F.R.Paiva 1461* (HUEFS); Pirituba, Porto Feliz, 11°45'20.9"S, 40°42'41.2"W, 710m, 11 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva 1400* (HUEFS); Planaltino, 13° 14'00.9"S, 40°21'24.2"W, 693m, 15 Oct 2012, *M.C.Machado & D.Cardoso 1288* (HUEFS); Planaltino, 13°11'24.9"S, 40°17'56.8"W, 784m, 15 Oct 2012, *M.C.Machado & D.Cardoso 1289* (HUEFS); Planaltino, 13°10'50.9"S, 40°14'54.1"W, 920m, 15 Oct 2012, *M.C. Machado & D.Cardoso 1290* (HUEFS); Planaltino, 13°10'50.9"S, 40°14'54.1"W, 920m, 15 Oct 2012, *M.C.Machado & D.Cardoso 1291* (HUEFS); Planaltino, 13°06'53.6"S, 40° 09'42.7"W, 842m, 15 Oct 2012, *M.C. Machado & D.Cardoso 1292* (HUEFS); Planaltino, 13°15'23.4"S, 40°21'49.7"W, 704m, 15 Oct 2012, *D.Cardoso & M.C.Machado 3264* (HUEFS); Planaltino, 13°11'24.9"S, 40°

- 17°56.8"W, 784m, 8 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva* 1329 (HUEFS); Planaltino, 13°11'24.9"S, 40°17'56.8"W, 784m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1330 (HUEFS); Planaltino, 13°11'24.9"S, 40°17'56.8"W, 784m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1331 (HUEFS); Planaltino, 13°14'00.9"S, 40°21'24.2"W, 693m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1332 (HUEFS); Planaltino, 13°14'00.9"S, 40°21'24.2"W, 693m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1333 (HUEFS); Planaltino, 13°14'00.9"S, 40°21'24.2"W, 693m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1334 (HUEFS); Planaltino, 13°07'19.6"S, 40°12'02.0"W, 908m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1335 (HUEFS); Poçoões, 14°32'01.4"S, 40°23'11.4"W, 796m, 23 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva* 1446 (HUEFS); Riachão do Jacuípe, 11°52'10.9"S, 39°18'47.0"W, 244m, 27 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva* 1472 (HUEFS); Ruy Barbosa, Estrada para Barro Duro, 12°18'04"S, 40°27'29"W, 387m, 14 Nov 2004, *L.P.Queiroz, T.A.B. Costa, D.Cardoso & A.Rapini* 9805 (HUEFS); Ruy Barbosa, 12°17'38.0"S, 40°27'43.2"W, 378m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1339 (HUEFS); Ruy Barbosa, 12°17'56.3"S, 40°27'27.9"W, 373m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1340 (HUEFS); Ruy Barbosa, 12°17'30.8"S, 40°27'58.1"W, 379m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1343 (HUEFS); Ruy Barbosa, 12°17'30.2"S, 40°27'58.2"W, 373m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1344 (HUEFS); Ruy Barbosa, 12°17'28.2"S, 40°28'00.6"W, 363m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva* 1345 (HUEFS); Ruy Barbosa, 12°18'55.0"S, 40°29'00.9"W, 366m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva* 1346 (HUEFS); Ruy Barbosa, 12°18'09.5"S, 40°31'11.2"W, 382m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva* 1347 (HUEFS); Ruy Barbosa, 12°18'07.8"S, 40°31'11.2"W, 393m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva* 1348 (HUEFS); Ruy Barbosa, 12°18'10.2"S, 40°31'12.7"W, 387m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1349 (HUEFS); Ruy Barbosa, 12°18'11.2"S, 40°31'12.8"W, 384m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1350 (HUEFS); Ruy Barbosa, 12°18'12.3"S, 40°31'13.4"W, 382m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva* 1351 (HUEFS); Ruy Barbosa, 12°18'12.3"S, 40°31'13.4"W, 382m, 9 Feb 2013, *M.C. Machado, F.M.Ferreira & T.T.S.Silva* 1352 (HUEFS); Ruy Barbosa, 12°18'13.1"S, 40°31'13.8"W, 378m, 9 Feb 2013, *M.C.Machado, F.M. Ferreira & T.T.S.Silva* 1353 (HUEFS); Ruy Barbosa, 12°18'16.0"S, 40°31'15.9"W, 391m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1354 (HUEFS); Ruy Barbosa, 12°18'21.7"S, 40°31'19.4"W, 396m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1355 (HUEFS); Ruy Barbosa, 12°22'33.8"S, 40°34'25.2"W, 447m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1356 (HUEFS); Ruy Barbosa, 12°22'05.2"S, 40°34'03.8"W, 408m, 9 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1357 (HUEFS); Santo Estêvão, 12°26'11.4"S, 39°13'21.3"W, 200m, 8 Feb 2013, *M.C.Machado, F.M.Ferreira & T.T.S.Silva* 1321 (HUEFS); Serrinha, 11°39'08.7"S, 38°59'33.6"W, 393m, 27 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva* 1475 (HUEFS); Tanquinho, 11°58'41.2"S, 39°08'35.2"W, 218m, 12 Aug 2012, *M.C.Machado, C. van den Berg, C.R. Buzatto & A.Sanguinetti* 1267 (HUEFS); Tucano, 10°54'09.9"S, 38°51'16.2"W, 225m, 31 Mar 2011, *M.C.Machado, J.G. Carvalho-Sobrinho & T.T.S.Silva* 1260 (HUEFS); Tucano, 10°53'58.1"S, 38°50'30.5"W, 234m, 28 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R. Paiva* 1477 (HUEFS); Tucano, 10°54'09.9"S, 38°51'16.2"W, 225m, 28 Mar 2013, *M.C.Machado, M.O.T.Menezes & F.R.Paiva* 1478 (HUEFS); Una, Estação Experimental da CEPLAC (ESMAI), Rodovia Una/Colônia/São José da Vitória, km 2, 12 Feb

2004, L.A.Mattos-Silva & B.R.Santos 5081 (HUESC, RB); Vitória da Conquista, 14° 51'22.3"S, 40°50'28.9"W, 895m, 24 Mar 2013, M.C.Machado, M.O.T.Menezes & F.R.Paiva 1447 (HUEFS); PERNAMBUCO: Bom Conselho, 09°10'31.3"S, 36°41' 40.9"W, 671m, 30 Mar 2013, M.C. Machado, M.O.T. Menezes & F.R.Paiva 1492 (HUEFS); Terezinha, 09°05'23.3"S, 36°39'45.6"W, 663m, 30 Mar 2013, M.C.Machado, M.O.T. Menezes & F.R.Paiva 1495 (HUEFS); SERGIPE: Canhoba, 10°08'22.7"S, 36°58'20.0"W, 33m, 29 Mar 2013, M.C.Machado, M.O.T. Menezes & F.R.Paiva 1486 (HUEFS).

Etymology:—named after the state of Bahia, Brazil, where the species is most common and probably has originated.

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