

TAXONOMY AND PHYLOGENY OF VIETNAMESE *SPONDIAS* L. (ANACARDIACEAE)

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ABSTRACT

Spondias is a small genus of Anacardiaceae. Vietnamese *Spondias* has remained taxonomically unresolved and the infrageneric relationship within the genus has been disputed. Here, we present molecular phylogenetic analyses of this genus and its close relatives using a combined dataset of the chloroplast *rbcL*, *matK*, and *trnL-F* regions. Molecular analyses strongly supported the monophyly of *Spondias* with two major clades and Vietnamese *Spondias* was placed within Asian *Spondias* clade. Based on both morphological and molecular data, we recognized two species of *Spondias*: *S. dulcis* Parkinson and *S. pinnata* (L. f.) Kurz in Vietnam. The key and description for Vietnamese *Spondias* species were provided. We also suggested to recognize *Spondias petelotii* as a synonym of *Allospodias lakonensis*.

Keywords: Molecular; Taxonomy; Phylogeny; *Spondias*; Synonym; Anacardiaceae

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NGHIÊN CỨU PHÂN LOẠI VÀ PHÁT SINH LOÀI CỦA CHI CÓC *SPONDIAS* L. (ANACARDIACEAE) Ở VIỆT NAM

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TÓM TẮT

Chi Cóc (*Spondias* L.) là một chi nhỏ của họ Xoài. Việc sắp xếp phân loại và tìm hiểu mối quan hệ di truyền của chi Cóc ở Việt Nam là chưa rõ ràng và còn tồn tại một số vấn đề. Nghiên cứu này tiến hành phân tích mối quan hệ phát sinh loài của chi Cóc và họ hàng gần gũi của chi này dựa trên dữ liệu sinh học phân tử là các đoạn gen lục lạp *rbcL*, *matK*, và *trnL-F*. Kết quả phân tích dữ liệu phân tử ủng hộ mạnh mẽ rằng chi Cóc là chi đơn phát sinh với hai nhánh phát sinh chính là nhánh Cóc Nam Mỹ và nhánh Cóc châu Á; Cóc Việt Nam nằm trong nhánh Cóc châu Á. Dựa trên cả dữ liệu phân tử và hình thái, nghiên cứu này ghi nhận Cóc Việt Nam bao gồm hai loài: *Spondias dulcis* Parkinson và *Spondias pinnata* (L. f.) Kurz. Khóa định loại và mô tả cho các loài Cóc Việt Nam được cung cấp. Nghiên cứu này cũng chỉ ra rằng *Spondias petelotii* là đồng nghĩa của *Allospodias lakonensis*.

Từ khóa: Phân tử; Phân loại; Phát sinh loài; *Spondias*; Đồng nghĩa; Anacardiaceae

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1. Introduction

Spondias L., the type genus of the subfamily Spondiadoideae Kunth ex Arn., is a small genus of fruit trees of Anacardiaceae with 18 species [1]. Members of *Spondias* are mainly distributed in tropical Asia, America and one species in Madagascar. The *Spondias* species show significant economic importance with various fruits that are used both as human and animal food [2].

The taxonomic history of *Spondias* was quite complex. *Spondias* was one of the first genera of Anacardiaceae described by Linnaeus with the type species *S. mombin* L. published in 1753 [1]. Bentham & Hooker (1862) [3] divided the family Anacardiaceae into two tribes, the Anacardieae and Spondieae. Subsequently, Marchand (1869) [4] published the tribe Spondiadeae (as Spondieae) and was the first to formulate a relatively modern concept of *Spondias*, in which he included *Evia* Blume, *Cytheraea* Wight & Arn. and *Wirtgenia* Jung. ex Hassk. On the other hand, of the taxa he either accepted in *Spondias* or recognized as synonyms of species in the genus, four are considered here to belong to other genera [4].

In the revision of tropical Asian *Spondias*, Airy-Shaw & Forman (1967) [5] lumped *Allospodias* and *Solenocarpus* with a rather broadly defined *Spondias*. In contrast, Kostermans (1981, 1991) defined the genera of the Spondiadoideae rather narrowly, maintaining *Allospodias* and *Solenocarpus*, transferring *Spondias philippinensis* (Elmer) Airy-Shaw and Forman to the latter, describing the new genus *Haplospodias* and formally returning the South Pacific species *Spondias dulcis* Parkinson into the pre-existing genus *Evia* Comm. ex Blume emend. Kosterm [6], [7].

Michell & Daly (2015) [1] suggested that *Allospodias lakonensis* (Pierre) Stapf (syn.: *Spondias lakonensis* Pierre var. *lakonensis*) should be removed from *Spondias* based on the structure of leaves and flowers such as: lack of an intramarginal vein and presence of perpendicular epimedial tertiary veins, styles connivent at anthesis and stigmas extrorse on the developing fruit, lack of a fibrous matrix on the endocarp. The morphology of *S.*

philippinensis is similar to the genus *Solenocarpus* such as: eucamptodromous secondary venation, single narrowly flabellate style, single stigma, unilocular ovary, strongly oblique fruit. Furthermore, *S. philippinensis* and *Solenocarpus indicus* Wight & Arn. morphologically share floral features such as: apert calyx, valvate corolla, single narrowly flabellate style. Thus, *Spondias philippinensis* should be kept out of *Spondias* and placed in *Solenocarpus*. In addition, *Haplospodias brandisiana* (Kurz) Kosterm. was considered as distinct from *Spondias* based on simple leaves without an intramarginal vein and a single style with an oblique stigma [1].

Michell & Daly (2015) [1] also discussed to *Solenocarpus indicus* and *Spondias dulcis*. They emphasized that the placement of *Spondias dulcis* in *Evia* is not correct, this species should be treated as a member of *Spondias* based on both morphological and molecular data; while, *Solenocarpus indicus* Wight & Arn. should be separated from *Spondias* [1]. Additionally, the situations of *Spondias philippinensis*, *Haplospodias brandisiana* and *Spondias bipinnata* are uncertain, but they are likely belonging to *Spondias* [1].

Min & Barfod (2008) [8] recognized two species of *Spondias* in China *S. pinnata* and *S. lakonensis*, in which *S. lakonensis* includes two varieties, *S. lakonensis* var. *lakonensis* and *S. lakonensis* var. *hirsuta*.

Chayamarit (1997) [9] studied phylogeny of Anacardiaceae (including *Spondias*) in Thailand based on molecular data. However, taxon sampling and sequences (only *rbcL*) of this study were limited. The result of the study showed close relationship between *Spondias* and *Dracontomelon*.

Silva et al., (2015) [2] conducted a phylogenetic study for neotropical species of the genus *Spondias*. Six species of *Spondias* from neotropic were sampled and three markers *rbcL*, *matK* and *trnH-psbA* spacer were applied. The result indicated that neotropical *Spondias* were divided into two clades. The first clade includes, *Spondias mombin* and *S. purpurea* L. while the second clade includes, *S. cytherea* Sonn., *S. tuberosa*

Arruda, *S. venulosa* (Engl.) Engl. and *Spondias* sp. However, *S. cytherea* was distributed widely in the world, thus the neotropical *Spondias* is likely not a monophyletic.

Nguyen (2004) [10] suggested that Vietnamese *Spondias* includes three species *S. cytherea*, *S. petelotii*, *S. pinnata* and is mainly distributed in some provinces of northern and southern Vietnam such as: Lang Son, Lai Chau, Son La, Hoa Binh, Lam Dong and Dong Nai. Members of Vietnamese *Spondias* have significantly economic uses and are widely planted. However, Pham (2003) [11] suggested that Vietnamese *Spondias* includes three species *S. pinnata*, *S. cythera* and *S. mombin*. Moreover, the author also noted that he did not observed *S. mombin* in Vietnam. Up to now, the studies of taxonomy and phylogeny of Vietnamese *Spondias* are limited, thus the relationship between *Spondia* species in Vietnam is still unclear and merits further morphological and molecular analyses.

The present study aims to: (1) infer the phylogenetic relationships within Vietnamese *Spondias*, (2) investigate the morphology and provide a phylogenetically based classification and integrating evidence from both molecular and morphological data.

2. Material and methods

2.1. Sampling, DNA extraction, amplification and sequencing

The present study sampled 14 species (16 individuals) including two genera *Spondias* and *Allospodias* (see Table 1) by using three chloroplast markers (*rbcL*, *matK* and *trnL-F*). Three species of the genus *Buchanania* were selected as outgroups (Table 1). Voucher information and GenBank accession numbers are listed in Table 1. Genomic DNA was extracted from silica gel dried tissues or herbarium material using the CTAB procedure [12]. Polymerase chain reactions and sequencing were performed using the primers used by Silva et al. (2015) [2], Le et al. (2018) [13] and Taberlet et al. (1991) [14]. We completed bidirectional sequencing using an ABI 3730 DNA Sequencer, performed quality estimation and assembly for the newly generated sequences with Geneious v.8.0.5

[15]. The sequences were aligned in Geneious v.8.0.5 [15].

2.2. Morphological analyses

The specimens or photos of specimens of *Spondias* from the following herbaria: HN, HNU, PE, HAL, TCD, L, C, A and KUN were examined. The herbarium code follow the Index Herbariorum (<http://sweetgum.nybg.org/ih/>). We also observed specimens from herbaria of department of Botany – Ha Noi Pedagogical University No. 2 (*) and National Institute of Medicinal Materials (**). Additionally, we examined living materials in the field.

2.3. Phylogenetic analyses

Both maximum likelihood (ML) and Bayesian inference (BI) methods were employed for the phylogenetic analyses of Vietnamese *Spondias*. The ML trees were generated by performing a rapid bootstrap analysis in RAxML v.8.2.8 [16], [17] with the GTR + I + G substitution model applying 1000 bootstrap replicates. The best-fitting models for the combined datasets were determined by the Akaike information Criterion (AIC) as implemented in jModelTest v.2.1.6 [18]. The Bayesian analysis was performed in MrBayes v.3.1.2 [19] on the CIPRES Science Gateway Portal [20] based on the same models as in the ML analysis. The Markov chain Monte Carlo (MCMC) algorithm was run for 5,000,000 generations with a total of four chains, starting from a random tree and trees were sampled every 1000 generations. The program Tracer v.1.6 [21] was used to check that effective sample sizes (ESSs) were attained for all relevant parameters assessed (> 200). With the first 25% of sampled generations discarded as burn-in, the 50% majority-rule consensus tree and Bayesian posterior probabilities (PP) were obtained using the remaining trees.

3. Results and discussion

Our study generated ten new sequences and produced a combined molecular dataset with 3194 aligned positions across all taxa. Phylogenetic trees from individual partitions resulted in lower resolution of relationships within Vietnamese *Spondias* than the combined dataset. The results from ML and

BI trees were highly congruent. Thus, we combined results in ML tree with BS and PP values. The phylogenetic relationships within *Spondias* by combined dataset are shown in Figure 1.

Our molecular results indicated that *Allospodias* is closely relative to *Spondias*.

Allospodias was recognized including two species *A. laxiflora* and *A. lakonensis*. However, according to *Flora of China*, Min & Barfod (2008) [8] recognized *Allospodias* as synonym of *Spondias* with *Spondias lakonensis* var. *lakonensis*. Pell et al. (2011) [16] recognized *Allospodias* as a separate genus in Anacardiaceae. Moreover, *Allospodias* can be distinguished from *Spondias* by the following characters: leaflets 11-23, often covered with hairs, without submarginal veins (vs. leaflets 5-11, glabrous on both sides, with submarginal veins in *Spondias*) (Figure 2); sepals minutely pubescent (vs. sepals glabrous in *Spondias*); drupes obovate to isodiametric (vs. drupes elliptic in *Spondias*). According to our morphological and molecular data, *Allospodias* was supported as a distinct genus from *Spondias* (Figures 1, 2). Thus, an updating for *Allospodias* in *Flora of China* is needed.

In the Checklist of plant species of Vietnam, Nguyen (2004) [10] recognized three species of *Spondias* in Vietnam including *S. petelotii* the species distributed in Dong Mo, Lang Son province. However, our sample of *Spondias petelotii* from Dong Mo, Lang Son (sample Le04 in Table 1) was placed in *Allospodias* with well supported molecular data (Figure 1). Furthermore, our morphological analyses suggest that morphology of *Spondias petelotii* is very close to *Allospodias lakonensis* such as: number of leaflets (11-23), without submarginal veins, flowers subtended by puberulent 0.5-1 mm bracts, ovary 4-locular, style 1, small fruit (Figures 2A, C, E; Figure 3). Thus, a re-treatment for *Spondias petelotii* as synonym of *Allospodias lakonensis* var. *lakonensis* is necessary, this study strongly suggested that *Spondias petelotii* is a synonym of *Allospodias lakonensis* based on both morphological and molecular evidences. Additionally, Pell et al. (2011) [22] suggested that *Allospodias laxiflora* could be

represented as a distinct genus due to differences in the connation of the stylodia (distinct), shape of stigmas (capitate), absence of endocarp lobing, number of locules and the absence of four parenchyma-filled cavities.

Spondias was well supported to be monophyletic group, two major clades were recognized within *Spondias*. The first clade includes American members with *Spondias testudinis* and *S. bahiensis* were being weakly supported as sister to the remaining members (Figure 1). The second clade consists of *Spondias radlkoferi*, *Spondias purpurea* from America plus Asian *Spondias*. The two species recognized in Vietnam *Spondias pinnata* and *Spondias dulcis* that were not placed together, but they were placed in Asian clade with strong support. Additionally, some Vietnamese documents still use the name *Spondias cytherea* Sonn. established in 1782 as accepted name, however that is not correct. This study suggests to use the accepted name *Spondias dulcis* Parkinson established in 1773. In addition, Pham (2003) [11] suggested that Vietnamese *Spondias* includes *Spondias mombin*. However, the author also noted that *S. mombin* was not observed in Vietnam. Mitchell & Daly (2015) [1] suggested that *Spondias mombin* is native to Mexico, south to SE Brazil. Furthermore, based on our molecular analyses, *S. mombin* does not belong to Asian members and placed in American clade. Thus, the recognition *S. mombin* in Vietnam is unstable. This study finally recognizes only two species of *Spondias* in Vietnam, *Spondias dulcis* and *Spondias pinnata*.

4. Taxonomic revision

Spondias L., Sp. Pl. 1: 371. 1753.

Type:—*Spondias mombin* L.

Description. Small trees. Leaves alternate, imparipinnately compound; leaflet margin serrate or entire. Inflorescence paniculate, terminal or axillary. Flowers 4(5) merous, bisexual or functionally unisexual. Stamens 8–10; filaments subulate to filiform, equal in length. Ovary 4(5) locular, with 1 ovule per locule; styles 4 or 5, free, or style 1. Fruit drupaceous; mesocarp juicy; endocarp woody or bony, covered by a fibrous matrix; embryo elongate, straight to slightly curved.

Distribution. According to Michell & Daly (2015) [1] *Spondias* includes 18 species, ten are native to the New World, distributed from Mexico to southern Brazil, one is native to Madagascar, seven are native to Asia and the South Pacific including two species in Vietnam.

Key to *Spondias* in Vietnam

Cultivated plants, flowers distinctly pedicellate; endocarp bearing numerous radiating, straight or curved, spinose processes; outer zone of fruit largely filled with parenchymatous tissue; no dense peripheral zone of longitudinally arranged fibres.....

Native plants, flowers subsessile; endocarp without radiating spinose processes, but with a dense smooth peripheral zone of longitudinally arranged fibres, interspersed with little parenchymatous tissue.....

Spondias dulcis Parkinson, J. voy. South Seas 39. 1773. **Type:**—TAHITI. (without date), Capt. Cook [Banks & Solander] s.n. (lectotype, BM-793299 n.v., designated by A. C. Smith 1985: 453).

≡ *Poupartia dulcis* (Parkinson) Blume, Bijdr. fl. Ned. Ind. 1161. 1826–27. *Evia dulcis* (Parkinson) Blume, Mus. Bot. 1(15): 233. 1850.

Spondias cytherea Sonn., Voy. Indes orient. 3: 242, t. 123. 1782.

Spondias dulcis var. *commersonii* Engl. in A. DC & C. DC., Monogr. phan. 4: 247. 1883.

Spondias dulcis var. *mucroserrata* Engl. in A. DC. & C. DC., Monogr. phan. 4: 247. 1883.

Spondias dulcis var. *integra* Engl. in A. DC. & C. DC., Monogr. phan. 4: 248. 1883.

Description:—Hermaphroditic trees, 10–25 m tall. Plant entirely glabrous except for some capitate glandular hairs. Leaves sometimes partially deciduous, 4–11 jugate, 15–60 cm long; petiole 9–15 cm long; lateral petiolules 2–11 mm long, basal lateral leaflets 5–7 × 1.5–3 cm, all laterals oblong or lanceolate to ovate. Inflorescences terminal and axillary, congested at branchlet apex, 9–32 cm long, secondary axes to 11.5 cm long; bracts 0.5–5 mm long, linear to lanceolate, linear to ovate; pedicel 1–3 mm long. Calyx 0.5–1.5 mm long, aestivation apert, divided nearly to base, the lobes 0.5–1 mm long, deltate; petals 2–3 ×

0.5–1.5 mm, oblong to ovate or deltate, cream-colored or white or whitish green, glabrous, reflexed at anthesis; stamens spreading, antesealous and antepetalous ones 2 and 1.5 mm long, respectively; the anthers 1 mm long; disk 0.5 mm tall, yellow; the stigmas obovate, slightly extrorse. Fruit 4–7 × 2.5–4 cm, ellipsoid, obovoid or oblong, maturing yellow or orange.

Distribution: Tropical area of the Neotropics, Asia, Australia.

Distribution in Vietnam: Widely cultivated in Vietnam.

Phenology in Vietnam: Flowering in Mar–May; fruiting in Jun–Dec.

Specimens examined: VIETNAM. Phu Tho: 21 August 2018, C.T. Le Le01 (*); Vinh Phuc: 23 August 2018, C.T. Le Le02 (*); Phu Tho: 26 August 2018, V.H. Nguyen & C.T. Le Le03 (*); Ha Noi: 2 November 1981, K.L. Phan P1831 (HNU); Lang Son: 28 April 1938, A. Petelok 6384 (HNU); 28 April 1938, A. Petelok 6384 (A). Peru. 1777, L.H. Ruiz s.n. (HAL); Thailand. Bangkok: April 1927, Kerr & G. Arthur Francis 12795A (TCD).

Spondias pinnata (L. f.) Kurz, Prelim. Rep. Forest Pegu, App. A, 44; App. B, 42. 1875.

Type: INDIA, (without date), König, J.G. ?, s.n.

Description: Small trees, branchlets glabrous. Petiole 12–16 cm; leaf blade 30–40 cm, imparipinnately compound with 5–11 opposite leaflets; leaflet petiolule 3–5 mm; leaflet papery, glabrous, base cuneate to rounded, lateral veins 12–25 pairs, slightly impressed adaxially, prominent abaxially, joined with submarginal collecting vein. Inflorescence terminal and axillary, glabrous, 25–35 cm. Flower sessile or subsessile, white, glabrous. Calyx lobes triangular, 0.5 mm. Petals ovate-oblong, 2.5 × 1.5 mm, apically acute. Stamens 1.5 mm. Ovary subglobose, ca. 1 mm; styles 4 or 5, free, ca. 0.5 mm. Drupe ellipsoid to elliptic-ovoid, yellowish orange at maturity, 3–5 × 2–3 cm; inner part of endocarp woody and grooved, outer part fibrous; with 2 or 3 seeds.

Distribution: China, Bhutan, Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, Singapore, Thailand and Vietnam.

Distribution in Vietnam: Lai Chau, Son La, Hoa Binh, Nghe An, Quang Nam, Gia Lai, Lam Dong, Ninh Thuan, Dong Nai,

Phenology in Vietnam: Flowering in Apr–Jun; fruiting in Aug–Sep.

Specimens examined: VIETNAM. Lai Chau: 13 October 2018, C.T. Le Le10 (*); 27 September 2000, D.K. Harder et al. DKH 5685 (HN); Tuyen Quang: 1 November 2003, N.Q. Binh & D.D. Cuong VN 1203 (HN); Gia Lai: 4 November 2002, T. Tuan 153 (**); CHINA. Yunnan: 18 October 2000, Y.M. Shiu & W.H. Chun 13125 (KUN); October 1936, C.W. Wang 79418 (KUN); August 1936, C.W. Wang 77690 (KUN); August 1936, C.W. Wang 77620 (PE); Hainan: 20 August 1929, F.A. McClure 704 (PE); 26 June 1936, S.K. Lau 27277 (KUN); 16 June 1932, S.K. Lau 98 (PE); INDIA: J.G. König s.n. (C); INDONESIA. Java: C.L. Blume s.n. (L).

5. Conclusion

The present study based on both morphological and molecular data supported that *Spondias* was closely relative to *Allospodias* with well supported. An updating for *Allospodias* in *Flora of China* was proposed. The present study recognized two *Spondias* species in Vietnam *Spondias dulcis* and *Spondias pinnata*; *Spondias petelotii* is synonym of *Allospodias lakonensis* var. *lakonensis* based on both morphological and molecular evidences.

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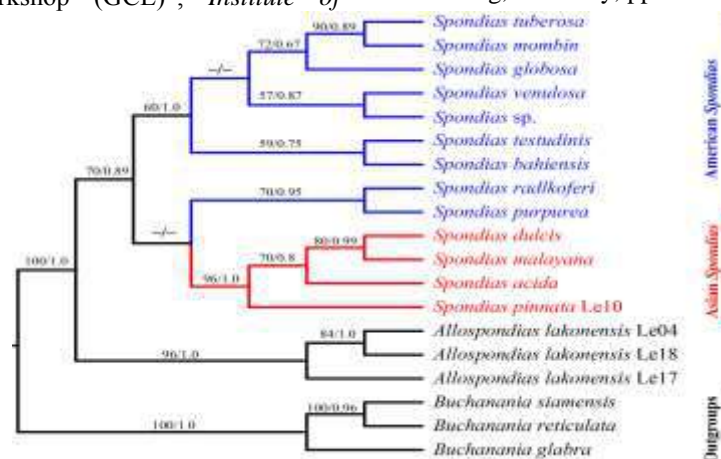


Figure 1. Phylogram of genus *Spondias* resulted from a maximum likelihood analysis with the combined data matrix. ML bootstrap values and posterior probabilities (PP) of the BI analysis are presented above the branches. “–” indicates the support values less than 50%

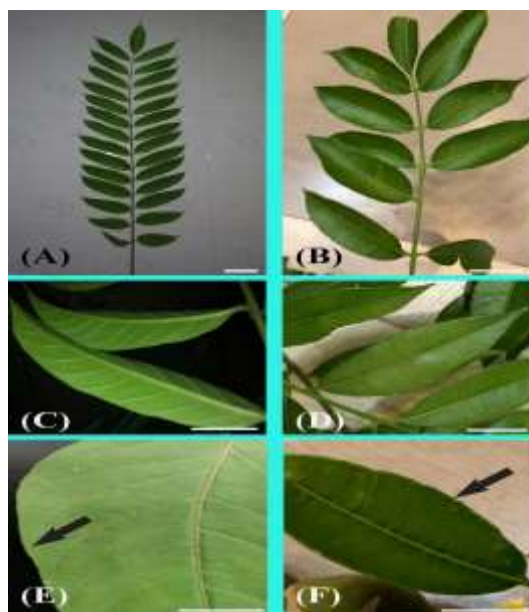


Figure 2. Leaf structure of *Allospondias* (A, C, E) and *Spondias* (B, D, F). A, B: number of leaflet; C, D: hair on leaf surface; E, F: submarginal vein. Scale bars = 1 cm



Figure 3. Isotype of *Spondias petelotii* (A) and *Allospondias laxiflora* (B)

(A: <https://plants.jstor.org/>; B: <http://www.cvh.ac.cn/>)

Table 1. Voucher information and GenBank accession numbers for DNA sequences generated or used in this study. The sequences generated in this study begin with MN, “–” indicates missing data

Species	Location	Voucher	matK	rbcL	trnLF
<i>Spondias tuberosa</i> Arruda	Brazil	W. Thomas s.n. (NY)	KP774614	KP774626	KP055577
<i>Spondias mombin</i> L.	USA; Costa Rica	Mitchell s.n. (NY); E. Roberto 528	KP774609	JQ590140	KP055575
<i>Spondias venulosa</i> (Engl.) Engl.	Brazil		KP774610	KP774632	KR081921
<i>Spondias purpurea</i> L.	Mexico	F. Arreola & F. Mora s.n.	KP774612	KP774619	KR081868
<i>Spondias</i> sp.	Brazil		KP774613	KP774630	–
<i>Spondias radlkoferi</i> Donn.Sm.	Brazil	R. Perez s.n.; E. Martinez S., C. H. Ramos, R. Lombero & G. Dominguez 25557	–	GQ981883	KR081870
<i>Spondias testudinis</i> J.D. Mitch. & D.C. Daly	Brazil	M. C. Machado & N. G. Antas 1563	–	–	KR081875
<i>Spondias malayana</i> Kosterm.	USA	Pell 775 (BKL)	–	–	KP055574
<i>Spondias globosa</i> J.D. Mitch. & D.C. Daly	Brazil	C. van den Berg 2171	–	–	KR081819
<i>Spondias bahiensis</i> P.Carvalho, Van den Berg & M.Machado	Brazil	E. Melo, M. C. Machado & B. M. Silva 11933	–	–	KR081811
<i>Spondias acida</i> Blume	Australia	D.A. Powell & H'ng Kim Chey 579	–	–	KR081767
<i>Spondias dulcis</i> Parkinson	Brazil	M. C. Machado, A. R. Barbosa & M. R. Santos 1302; Weiblen, G. D. WS5B0380	KP774606	JF739148	KR081815
<i>Spondias pinnata</i> (Koenig ex L.f.) Kurz	Lai Chau, Vietnam	C.T. Le Le10	MN262106	MN262109	MN262102
<i>Allospodias lakonensis</i> Stapf	Lang Son, Vietnam	C.T. Le Le04	MN262104	MN262107	MN262100
<i>Allospodias lakonensis</i> Stapf	Vinh Phuc, Vietnam	C.T. Le Le18	MN262105	MN262108	MN262101
<i>Allospodias lakonensis</i> Stapf	Vietnam	C.T. Le Le17	–	–	MN262103
<i>Buchanania glabra</i> Wall. ex Engl.	Vietnam	Pell 1062 (NY)	–	–	KP055491
<i>Buchanania siamensis</i> Miq.	Vietnam	Pell 1054 (NY); Toyama et al. 554 (KYUM)	AB925072	AB925701	KP055493
<i>Buchanania reticulata</i> Hance	Vietnam; Cambodia	Pell 1057 (NY); Toyama et al. 167 (KYUM)	AB924829	AB925441	KP055492