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Taxonomy and phylogenetic insights for Mexican and Central American species of *Acer* (Sapindaceae)[1]

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Abstract. The understanding of the species traits of *Acer* L. growing in subtropical and tropical America is relevant because this region represents its most southern geographic range in the hemisphere. This study evaluates the morphological variation and updates the taxonomic status, distribution, and phylogenetic relationships of *Acer* in Middle America. A total of eight taxa are recognized. The presence of *Acer negundo* subsp. *mexicanum* is documented for Honduras, while five taxa are restricted to northern Mexico (*Acer negundo* var. *arizonicum*, *A. negundo* var. *texanum*, *Acer glabrum* var. *neomexicanum*, *Acer grandidentatum*, *Acer grandidentatum* var. *sinuosum*), whereas *Acer binzayedii* is endemic to western Mexico. Only *Acer skutchii* and *A. negundo* subsp. *mexicanum* are widely distributed in the investigated area. The populations are often fragmented and disjunct. The phylogenetic analysis identifies the *A. grandidentatum* populations from northwestern Mexico as a separate lineage. Descriptions, distribution maps, photographs, and conservation assessments of the species as well as a key to species are provided.

Key words: *Acer binzayedii*, *Acer glabrum*, *Acer grandidentatum*, *Acer negundo*, *Acer skutchii*, Guatemala, Honduras, Sapindales, sugar maple

Acer L. and its related genus *Dipteronia* Oliv., formerly placed in Aceraceae Juss., are part of the Sapindaceae Juss. family, Order Sapindales Berchtold & J. Presl (APG 1998, 2003, 2009, 2016). Traditionally, Sapindaceae was treated as distinct from the families Aceraceae and Hippocastanaceae A. Rich. Former Aceraceae can be distinguished by petals without scales and bicarpellate ovaries *versus* petals with scales in Sapindaceae (de Jong 1976) and tricarpellate ovaries in most of the Sapindaceae members. Using molecular data, the three families have been united, adopting a broader concept and ensuring monophyly (APG 2009, 2016; Buerki *et al*. 2009). According to molecular data, *Acer* and *Dipteronia* are classified within the tribe Acereae (Durande) Dumort., subfamily Hippocastanoideae Burnett (Harrington *et al*. 2005)

Acer is distributed in temperate, subtropical, and tropical areas of the Northern Hemisphere (van Gelderen *et al*. 1994). In the American Northern Hemisphere, the genus is present in temperate regions of Canada, the southernmost part of Alaska, the continental USA, and montane regions of Mexico and Central America (Wolfe and Tanai 1987, van Gelderen *et al*. 1994, Vargas-Rodriguez and Platt 2012). The fossil record indicates that the group was highly diversified in western USA during the Paleogene and early Neogene, including *Dipteronia* species (a closely related genus), which are now found only in China (Wolfe and Tanai 1987, McClain and Manchester 2001).

Taxonomic treatments and classifications of the North American species have been developed since the 19th century (Nicholson 1881; Wesmael 1890; Sargent 1891a, 1891b, 1902; Rehder 1927, 1933, 1949; Keller 1942; Desmarais 1952; Brizicky 1963; Ellis 1963; Delendick 1981). The inflorescence, insertion of the stamens in the disc, sexual expression, leaf types, and chemistry of flavonoids are characters used in the infrageneric classifications (Brizicky 1963, de Jong 1976, Delendick 1981). The characters were reviewed by de Jong (in van Gelderen *et al*. 1994), who rearranged some sections and series and identified

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eight groups (out of 16) in the American continent: *Acer*, *Glabra* Pax, *Lithocarpa* Pax, *Macrantha* Pax, *Negundo* (Boehmer) Maximowicz, *Palmata* Pax, *Parviflora* Koidzumi, and *Rubra* Pax.

The taxonomic treatments also distinguish species with many varieties or geographic subspecies. This is the case, for example, of *Acer saccharum* Marshall (Desmaris 1952), *Acer glabrum* Torr. (Keller 1942), and *Acer negundo* L. (Wesmael 1890). The descriptions of many of the subspecies and varieties from these species were based on the morphology of leaves and fruits (especially the angle between the wings) and geographic distribution. Desmaris (1952) studied leaf characters in *A. saccharum* and related taxa—known as *Acer floridanum*, *Acer grandidentatum*, *Acer leucoderme*, and *Acer nigrum*—and treated them as subspecies of *A. saccharum*. This concept was accepted by Murray (1970) and de Jong (1976) and adopted by van Gelderen *et al*. (1994). The shape and size of leaves were used to propose infraspecific categories of *A. glabrum* (Keller 1942, Murray 1981), and most of these categories were later used by van Gelderen *et al*. (1994). Murray (1975, 1980b, 1981) created subspecies, varieties, and forms within *A. negundo* based on branch color and leaf pubescence, but not all categories were maintained later on (van Gelderen *et al*. 1994).

The most recent taxonomic synopsis of *Acer* includes nine species with subspecies and varieties that are distributed on the American continent (van Gelderen *et al*. 1994). The recently described *Acer binzayedii* Vargas-Rodriguez raises the number of species in this continent to 10 (Vargas-Rodriguez *et al*. 2017b). The treatment by van Gelderen *et al*. (1994) contains the following:

- *Acer spicatum* Lam. (section *Parviflora*, series *Caudata* Pax);
- *Acer circinatum* Pursh (section *Palmata*, series *Palmata*);
- *Acer pensylvanicum* L. (section *Macrantha*);
- *Acer glabrum* Torr. subsp. *glabrum*, *A. glabrum* subsp. *diffusum* (Greene) Murray, *A. glabrum* subsp. *douglasii* (Hook.) Wesm., *A. glabrum* subsp. *neomexicanum* (Greene) Murray, *A. glabrum* var. *greenei* Keller, *A. glabrum* var. *torreyi* (Greene) Smiley (section *Glabra*, series *Glabra*);
- *Acer negundo* L. subsp. *negundo*, *A. negundo* subsp. *californicum* (Torr. & Gray) Wesm., *A. negundo* subsp. *interius* (Britton) Löve & Löve, *A. negundo* subsp. *mexicanum* (DC.) Wesm., *A. negundo* var. *texanum* Pax (section *Negundo*, series *Negundo*);
- *Acer saccharum* Marshall subsp. *saccharum*, *A. saccharum* subsp. *floridanum* (Chapm.) Desmarais, *A. saccharum* subsp. *grandidentatum* (Torr. & Gray) Desmarais, *A. saccharum* subsp. *leucoderme* (Small) Desmarais, *A. saccharum* subsp. *nigrum* (Michx.) Desmarais, *A. saccharum* subsp. *ozarkense* Murray, *A. saccharum* subsp. *skutchii* (Rehder) Murray, *A. saccharum* var. *rugelii* (Pax) Rehder, *A. saccharum* var. *schneckii* Rehder, *A. saccharum* var. *sinuosum* (Rehder) Sarg. (section *Acer*, series *Saccharodendron* (Rafinesque) Murray);
- *Acer macrophyllum* Pursh (section *Lithocarpa*, series *Macrophylla*);
- *Acer rubrum* L. (section *Rubra*); and
- *Acer saccharinum* L. (section *Rubra*).

The subspecific classification proposed by van Gelderen *et al*. (1994) has not been widely accepted by authors. For instance, on the basis of anther ornamentation, perianth and anther length, fruit size and shape, length of wing and its sulcus, and leaf trichome ornamentation, *A. saccharum* subsp. *skutchii* has been raised to the species status (Vargas-Rodriguez *et al*. 2017b). Justice (1995) treats the North American members of the *Glabra* series as varieties, using leaf characters, such as the veins, the size of the sinus and teeth, and the areole development. The present work follows the infraespecific classification proposed by van Gelderen *et al*. (1994) for sections and series and as a primary reference to examine the status of the subspecies, varieties, and forms.

The taxonomic status, distribution, and phylogenetic relationships of the *Acer* species in the American tropics are poorly known. The "Flora of Guatemala" reports the presence of *A. skutchii*, *A. negundo* var. *orizabense*, and *A. negundo* var. *mexicanum* in Guatemala (Standley and Steyermark 1949). Murray (1980a) corroborates the presence of both species in Guatemala but recognizes only *A. negundo* subsp. *mexicanum* and describes forma *mexicanum* and forma *glabrescens* within *A. negundo* subsp. *mexicanum* (Murray 1980b). Regional floras from the states of Michoacán and Veracruz also identify the infraspecific category *mexicanum* either as a subspecies or as a variety (Cabrera-Rodríguez 1985, Calderón de Rzedowski 2001). The occurrence of *A. saccharum* subsp. *grandidentatum* in Mexico was also documented by Murray (1980b). Gibbs and Chen (2009) address a global conservation assessment of maples and recognize the presence of *A. negundo* subsp. *mexicanum* and *A. skutchii* in Mexico and Guatemala and *A. grandidentatum* in Mexico. A recent list of endangered trees occurring in Mexico also identifies *A. grandidentatum*, *A. negundo* subsp. *mexicanum*, and *A. skutchii* in the country (González-Espinosa *et al*. 2011). Only *A. saccharum* subsp. *skutchii* and the recently described *A. binzayedii* have been the subject of ecological and genetic studies (Vargas-Rodriguez and Platt 2012, Vargas-Rodriguez *et al*. 2015). Scattered herbarium material has been collected for other *Acer* species growing in Mexico and Central America, but the number of species, morphological variation, and their geographic distribution have not been evaluated thoroughly. The distribution of the genus in tropical America becomes relevant because this region represents its most southern geographic range on the continent, with populations that are often fragmented and disjunct, raising concerns about their conservation status (Vargas-Rodriguez and Platt 2012).

This study aims to (a) address the taxonomic status of *Acer* species distributed in Mexico and Central America, (b) discuss the morphological variation of the species present in Mexico and Central America, (c) update the species' geographic distribution, and (d) explore the phylogenetic relationships of the species from Mexico and Central America using data from the ribosomal internal transcribed spacer (ITS) and the chloroplast intergenic regions *ndhF–rpl32R* and *psbJ–petA*.

Materials and Methods. Approximately 1,105 herbarium specimens and available types of *Acer* were examined from the following collections: A, AGUAT, ARIZ, BIGU, BM, EAP, ECON, F, GH, GUAT, HEH, IBUG, IEB, K, LL-TEX, LSU, MEXU, MICH, MO, NCU, NY, P, RM, TEFH, TENN, UNM, US, USCG, UVAL, WIS, XAL, ZEA (Thiers, continuously updated). In addition to specimens from Mexico and Central America, the examined specimens included collections from several locations in western, central, and eastern USA deposited in the above-listed herbaria. Material from the USA was used to examine species variation; however, morphological descriptions of the taxa presented here were based on Mexican and Central American specimens. Original descriptions from all studied taxa were reviewed. Examined specimens are listed alphabetically by country, state or department, and municipality. Field collections and observations were performed in Mexico and Guatemala and the samples were deposited in the LSU herbarium. Species distribution maps were made using the geographic coordinates from herbarium labels and from personal collections; the data were plotted in R using the ggplot2 and maptools packages (R Core Team 2013).

Morphology was characterized and measured following the terminology of Wolfe and Tanai (1987) for fruits, Anderson and Hubricht (1938) for leaves, and Krause (1982) for trichome ornamentation. Flowers from herbarium specimens were rehydrated using aerosol OT (Ayensu 1976). Measurements and observations of flowers, buds, and leaf ornamentation were made using an Olympus SZX12 dissecting stereo microscope (Tokyo, Japan), and leaf size was measured with a caliper. Dried pollen and leaf material was coated with gold:palladium (60:40) in an Edwards S-150 sputter coater (Edwards High Vacuum Co. International, Wilmingotn, MA) and observed using a Cambridge S-260 scanning electron microscope. Complete reproductive structures were lacking in some herbarium specimens; thus, the description of flowers and/or fruits were omitted for those species.

Taxon Sampling. The infrageneric classification follows van Gelderen *et al*. (1994) for sections and series. The subspecies, variety, and forma statuses were first examined and contrasted using van Gelderen *et al*. (1994).

A total of 168 accessions of *Acer,* 112 newly obtained, representing 81 taxa and 15 sections (*sensu* van Gelderen *et al*. 1994) were included in the phylogenetic study (Table 1). *Acer saccharum* subsp. *skutchii* was sampled from two populations from Mexico and Guatemala, *A. binzayedii* from two populations in Mexico, *A. negundo* from four disjunct localities in the USA and 11 sites from Mexico and Guatemala, and *A. saccharum* subsp. *grandidentatum* from seven and *A. glabrum* from three populations in the USA and Mexico (Table 1). Sequences from the species of the *Saccharodendron* series, *Acer* section (sugar maples), were also obtained and included in the analysis: *A. saccharum* subsp. *floridanum* (four samples), *A. saccharum* subsp. *leucoderme* (three samples), *A. saccharum* subsp. *nigrum* (two samples), and *A. saccharum* subsp. *saccharum* (eight samples) (Table 1). Accessions from different sections (67)

Table 1. Taxa included in the phylogenetic analyses. Sectional treatment follows van Gelderen *et al*. (1994). North American species are in bold. Samples with the nuclear ribosomal DNA internal transcribed spacer region newly sequenced or obtained from GenBank are presented below. Amplified sequences of the *psbJ–petA* and *rpl32R–ndhF* chloroplast regions are denoted by an asterisk (*).

Section	Series	Species	GenBank accession number	Voucher data	Source
		**Aesculus pavia*	MN043343	Vargas-Rodriguez s.n. LSU	This work
		**Dipteronia sinensis*	MN043339	Zho *et al*. 2478 PE	This work
		Koelreuteria sp.	EU720547		Buerki *et al*. 2009
		* *Koelreuteria paniculata*	KY859413		Kim *et al*. 2018
		Sapindus delavayi	AY207570		Tian *et al*. 2002
Acer	*Acer*	*A. caesium* subsp. *caesium*	AY605293		Grimm 2003
		A. heldreichii subsp. *heldreichii*	AY605301		Grimm 2003
		A. heldreichii subsp. *trautvetteri*	AF401126		Tian *et al*. 2002
		A. pseudoplatanus	AF241500		Suh *et al*. 2000
		A. velutinum	AY605356		Grimm 2003
Acer	*Monspessulana*	*A. hyrcanum* subsp. *hyrcanum*	AY605305		Grimm 2003
		A. hyrcanum subsp. *hyrcanum*	DQ366130		Grimm 2003
		A. monspessulanum subsp. *monspessulanum*	AF401127		Tian *et al*. 2002
		A. obtusifolium	AM238327		Grimm *et al*. 2007
		A. opalus subsp. *opalus*	AF401128		Tian *et al*. 2002
		A. sempervirens	AY605351		Grimm 2003
Acer	*Saccharodendron*	***A. binzayedii***	MN043321	Vargas-Rodriguez 850 LSU; Jalisco	This work
		A. binzayedii	FJ906754.1	Vargas-Rodriguez 371 LSU; Jalisco	This work
		A. binzayedii	MN027948	Vargas-Rodriguez 527 LSU; Guerrero	This work
		A. binzayedii	KT933360.1	Vargas-Rodriguez 532 LSU; Guerrero	Vargas-Rodriguez 2015
		A. binzayedii	MN043330	Vargas-Rodriguez 543 LSU; Guerrero	This work
		A. grandidentatum	DQ366134		Grimm *et al*. 2006
		A. grandidentatum	MN043331	Bravo 842 IEB; Chihuahua	This work
		A. grandidentatum	MN043335	Tucker 2570 A; Chihuahua	This work
		A. grandidentatum	MN043334	Jercinovic 831 UNM; New Mexico	This work
		A. grandidentatum	MN043337	Felger *et al*. 92-791 ARIZ; Sonora	This work
		A. grandidentatum	MN043332	van Devender 95-394 LL TEX; Sonora	This work
		A. grandidentatum	MN043336	Felger and Layne 93-505 LL TEX; Sonora	This work
		A. grandidentatum	MN043333	Martin *et al*. s.n. ARIZ; Sonora	This work

Table 1. Continued.

Section	Series	Species	GenBank accession number	Voucher data	Source
		A. grandidentatum	MN027945	Heil *et al*. 01-1220 UNM; Utah	This work
		****A. grandidentatum***	MN027946 MN043338	Clark 11918 UNM; Arizona	This work
		A. grandidentatum	MN027947	Carr 24 UNM; Arizona	This work
		****A. grandidentatum* var. *sinuosum***	MN043324	Villarreal *et al*. 9108 LL TEX; Nuevo León	This work
		****A. grandidentatum* var. *sinuosum***	MN043323	Villarreal 8738 MO; Coahuila	This work
		****A. grandidentatum* var. *sinuosum***	MN043326	Burleson *et al*. 2325 LL TEX; Coahuila	This work
		****A. grandidentatum* var. *sinuosum***	MN043322	Carranza *et al*. 2075 LL TEX; Coahuila	This work
		****A. grandidentatum* var. *sinuosum***	MN027956 MN043325	Johnston *et al*. 12035K LL TEX; Coahuila	This work
		A. grandidentatum* var. *sinuosum	MN027960	Briones 1191 MO; Tamaulipas	This work
		A. grandidentatum* var. *sinuosum	MN027949	Chauvin 06YC180-T2 UNM; Texas	This work
		****A. grandidentatum* var. *sinuosum***	MN043327	s.n. 7192 UNM; New Mexico	This work
		****A. saccharum***	MN027954 MN043312	Vargas-Rodriguez 1013 LSU; Vermont	This work
		A. saccharum	MN027959	Vargas-Rodriguez 1064 LSU; New York	This work
		A. saccharum	KT933395.1 MN027955	Vargas-Rodriguez 1204 LSU; Illinois	Vargas-Rodriguez 2015
		A. saccharum	MN027952	Vargas-Rodriguez 1685 LSU; Ohio	This work
		****A. saccharum***	MN043313	Vargas-Rodriguez 1101 LSU; Pennsylvania	This work
		****A. saccharum***	MN043316	Vargas-Rodriguez 1503 LSU; Alabama	This work
		A. saccharum	MN027950	Vargas-Rodriguez 1568 LSU; Tennessee	This work
		****A. saccharum***	KT933372.1	Vargas-Rodriguez 1621 LSU; Tennessee	Vargas-Rodriguez 2015
		A. saccharum* subsp. *floridanum	DQ366139		Grimm *et al*. 2006
		****A. saccharum* subsp. *floridanum***	MN043317	Urbatsch s.n. LSU; Louisiana	This work
		A. saccharum* subsp. *floridanum	MN027957	Givens 3611 LSU; Louisiana	This work
		****A. saccharum* subsp. *floridanum?***	MN027958 MN043318	Langdon s.n. LSU; Tennessee	This work
		A. saccharum* subsp. *leucoderme	MN027953	Givens 5315 LSU; Georgia	This work
		****A. saccharum* subsp. *leucoderme***	MN043329	Haynes 10404 LSU; Alabama	This work
		****A. saccharum* subsp. *leucoderme***	MN043315	Super s.n. LSU; Tennessee	This work
		****A. saccharum* subsp. *nigrum?***	MN043314	Peet s.n. LSU; South Carolina	This work
		****A. saccharum* subsp. *nigrum***	MN043319	Downs 2206 NCU; West Virginia	This work

Table 1. Continued.

Section	Series	Species	GenBank accession number	Voucher data	Source
		***A. skutchii**	MN043320	Vargas-Rodriguez 1463 LSU; Guatemala	This work
		A. skutchii	FJ906755.1	Vargas-Rodriguez 390 LSU; Tamaulipas	This work
		***A. skutchii**	MN043328	Vargas-Rodriguez 599 LSU; Tamaulipas	This work
Ginnala		*A. tataricum* subsp. *tataricum*	AF401146		Tian *et al*. 2002
Glabra	*Glabra*	***A. glabrum***	AF401139		Tian *et al*. 2002
		***A. glabrum** **var.** **glabrum**	MN027943 MN043341	Rief 5409 LSU; New Mexico	This work
		***A. glabrum** **var.** **douglasii**	MN027944 MN043342	Burckhater 2666 LSU; Colorado	This work
		***A. glabrum** **var.** **neomexicanum**	MN027942 MN043340	Benitez 1465 MEXU; Chihuahua	This work
Glabra	*Arguta*	*A. acuminatum*	AY605371		Grimm 2003
		A. argutum	AF401153		Tian *et al*. 2002
		A. barbinerve	AJ634569		Grimm 2003
Hyptiocarpa		*A. laurinum*	AF401149		Tian *et al*. 2002
		A. laurinum	AF241490		Suh *et al*. 2000
Lithocarpa	*Lithocarpa*	*A. diabolicum*	AF241484		Suh *et al*. 2000
		A. sterculiaceum subsp. *sterculiaceum*	DQ366144		Grimm *et al*. 2006
Lithocarpa	*Macrophylla*	***A. macrophyllum***	MN027961	Fujinami 234 LSU; California	This work
Macrantha		*A. capillipes*	DQ238371		Grimm *et al*. 2006
		A. caudatifolium	DQ238380		Grimm *et al*. 2006
		A. crataegifolium	DQ238378		Grimm *et al*. 2006
		A. davidii spp. *davidii*	DQ238364		Grimm *et al*. 2006
		A. micranthum	AF020369		Ackerly and Donoghue 1998
		A. morifolium	HM008384		Zhang *et al*. 2010
		A. pensylvanicum	AF241497		Suh *et al*. 2000
		A. rufinerve	DQ238374		Grimm *et al*. 2006
		A. tegmentosum	U89907		Cho *et al*. 1997
		A. sikkimense subsp. *sikkimense*	HM008387		Zhang *et al*. 2010
		A. tschonoskii	AF020372		Ackerly and Donoghue 1998
Negundo	*Negundo*	***A. negundo***	DQ238361		Grimm *et al*. 2006
		A. negundo	MN027928	Vargas-Rodriguez 561 LSU; Louisiana	This work
		A. negundo	MN027929	Hunter 9 LSU; Arkansas	This work
		A. negundo	MN027930	Vargas-Rodriguez 1143 LSU; Michigan	This work
		A. negundo **var.** ***arizonicum***	MN027931	Henrickson 11448 LL TEX; Coahuila	This work

Table 1. Continued.

Section	Series	Species	GenBank accession number	Voucher data	Source
		A. negundo* var. *californicum	MN027941	Thomas 7672 LSU; California	This work
		A. negundo* subsp. *mexicanum	MN027936	Lopez 95 IEB; Hidalgo	This work
		A. negundo* subsp. *mexicanum	MN027932	Vargas-Rodriguez 797 LSU; Chiapas	This work
		A. negundo* subsp. *mexicanum	MN027933	Torres 13506 XAL; Michoacán	This work
		A. negundo* subsp. *mexicanum	MN027940	Ortiz 1 IBUG; Jalisco	This work
		A. negundo* subsp. *mexicanum	MN027938	Garcia 9 IBUG; Jalisco	This work
		A. negundo* subsp. *mexicanum	MN027939	Rzedowski 26708 ARIZ; Edo. Mexico	This work
		A. negundo* subsp. *mexicanum	MN027934	Rzedowski 32775 NY; Cd. Mexico	This work
		A. negundo* subsp. *mexicanum	MN027937	Nee 26791 NY; Veracruz	This work
		A. negundo* subsp. *mexicanum	MN027935	Vargas-Rodriguez 1487 LSU; Guatemala	This work
		A. negundo* var. *texanum	MN027927 MN027951	Villarreal 2762 LL TEX; Nuevo León	This work
Negundo	*Cissifolia*	*A. cissifolium*	AF241483		Suh *et al*. 2000
Palmata	*Palmata*	***A. circinatum***	AF020373		Ackerly and Donoghue 1998
		A. palmatum subsp. *palmatum*	AF401123		Tian *et al*. 2002
		A. pseudosieboldianum subsp. *pseudosieboldianum*	AF241501		Suh *et al*. 2000
		A. pseudosieboldianum subsp. *takeshimense*	AF241504		Suh *et al*. 2000
		A. pubinerve	AF401125		Tian *et al*. 2002
Palmata	*Penninervia*	*A. crassum*	AF401135		Tian *et al*. 2002
		A. fabri	AF241486		Suh *et al*. 2000
	Caudata	***A. spicatum***	AY605431		Grimm *et al*. 2006
Palmata	*Sinensia*	*A. miaoshanicum*	AF401124		Tian *et al*. 2002
Parviflora	*Distyla*	*A. distylum*	DQ238354		Grimm *et al*. 2006
	Parviflora	*A. nipponicum*	AF401157		Tian *et al*. 2002
Pentaphylla	*Pentaphylla*	*A. pentaphyllum*	AF401137		Tian *et al*. 2002
		A. poliophyllum	AF401134		Tian *et al*. 2002
Pentaphylla	*Trifida*	*A. albopurpurascens*	DQ238471		Grimm *et al*. 2006
		A. buergerianum	AF401133		Tian *et al*. 2002
		A. paxii	AF401132		Tian *et al*. 2002
Platanoidea		*A. campestre*	AF020382		Ackerly and Donoghue 1998
		A. mono subsp. *mono*	DQ238447		Grimm *et al*. 2006
		A. platanoides	DQ238461		Grimm *et al*. 2006
Pubescentia		*A. pilosum*	DQ238345		Grimm *et al*. 2006

Table 1. Continued.

Section	Series	Species	GenBank accession number	Voucher data	Source
Rubra		***A. rubrum***	AY605461		Grimm 2003
		A. saccharinum	AF401151		Tian *et al*. 2002
		A. pycnanthum	AM113528		Grimm *et al.* 2006
Trifoliata	*Grisea*	*A. griseum*	AF401131		Tian *et al*. 2002
		A. maximowiczianum	DQ238484		Grimm *et al.* 2006
		A. triflorum	AF401130		Tian *et al*. 2002
Trifoliata	*Mandshurica*	*A. mandshuricum*	AF401129		Tian *et al*. 2002
Wardiana		*A. wardii*	AF401159		Tian *et al*. 2002

were obtained from GenBank (Table 1). Multiple accessions for species and geographic regions were included to improve resolution of the relationships among closely related individuals. Sequences of *Dipteronia sinensis* Oliv. and *Aesculus pavia* L. (Hippocastaneae) were included in the chloroplast dataset to improve resolution of Acereae. *Koelreuteria* sp. Laxm. (Sapindaceae) was used as outgroup in all phylogenetic analyses. In addition, *Sapindus delavayi* Radlk. was used as outgroup species in the ITS-based analyses.

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING. Total DNA was extracted from silica gel–dried leaves or from herbarium material. Approximately 20–50 mg of dry leaf material was ground using a Mini Beadbeatter 8 (BioSpec Products, Bartlesville, OK). Total genomic DNA was extracted and purified using a DNeasy Plant Mini kit (Qiagen, Valencia, CA) following the manufacturer's protocol. Polymerase chain reaction amplifications were performed in 25-μL aliquots containing 20 ng of genomic DNA, 0.2 mM dNTP, 10 μL of each primer, 1.5 mM $MgCl_2$, and 1 U HotStarTaq polymerase (HotStarTaq Master Mix, Qiagen). Cycling conditions for DNA amplification consisted of an initial denaturation at 95 °C for 15 min, followed by 30 cycles of amplification as follows: (a) 10 cycles of denaturation at 94 °C for 1 min, annealing at 55 °C for 1 min, and extension at 72 °C for 1 min; and (b) 20 cycles of denaturation at 94 °C for 1 min, annealing at 50 °C for 1 min, and extension at 72 °C for 1.5 min. The cycle ended with a final extension at 72 °C for 7 min. The ITS region was amplified in two successive PCR reactions. The first reaction used a set of external primers, ITS-18 (Urbatsch *et al*. 2000) and ITS-4 (White *et al*. 1990). The amplicons from the first reaction were directly used in the second amplification with nested primers ITS-1 (Urbatsch *et al*. 2000) and ITS-4. In addition, the *ndhF–rpl32R* intergenic spacer in the small single-copy region and *psbJ–petA* intergenic spacer in the large single-copy region from the chloroplast were amplified (Shaw *et al*. 2007). Cycling conditions for chloroplast DNA amplification followed Shaw *et al*. (2007).

The ITS and chloroplast PCR products were purified and sequenced in both directions using a BigDye Terminator v3.1 (Applied Biosystems, Foster City, CA) on an ABI-PRISM 3730XL (Applied Biosystems).

SEQUENCE ALIGNMENT AND PHYLOGENETIC RECONSTRUCTION. Obtained sequence chromatograms were visually inspected and edited with Sequencher v4.1 (Gene Codes Corporation, Ann Arbor, MI). The alignment was done using the online version of GUIDANCE2 (Sela *et al*. 2015) and the MAFFT algorithm, with five iterations and 100 bootstrap replicates. Sequences were manually adjusted in McClade v4.08 (Maddison and Maddison 2000) as needed. The chloroplast datasets of the *ndhF–rpl32R* and *psbJ–petA* intergenic spacers were concatenated. Accession numbers of sequences submitted to GenBank are included in Table 1. The best-fit nucleotide substitution model was estimated using MrModeltest v2.3 (Nylander 2004). The GTR + G model was chosen under the Akaike Information Criterion for the ITS dataset and the GTR substitution model for the chloroplast dataset.

A Bayesian inference of the ITS and chloroplast datasets was performed using MrBayes 3.2.1 (Ronquist and Huelsenbeck 2011). The two datasets were each subjected to two independent Bayesian analyses. Each run consisted of 2×10^7 generations of Markov Chain Monte Carlo with the default of one cold and three heated chains, and the sampling was conducted every 2,000 generations with four independent runs, starting from independently generated random trees. The burn-in consisted of 25% of trees. Convergence and mixing of the runs and effective sample size of parameter estimates were assessed using Tracer v1.6 (Rambaut *et al*. 2014). The produced runs were combined using LogCombiner v1.8 (Drummond *et al*. 2012). The combined trees were summarized with a maximum clade credibility tree and branch lengths using mean heights with TreeAnnotator v1.8 (Drummond *et al*. 2012). The final trees were visualized in FigTree v1.4.3 (Rambaut 2012).

Results. The taxonomic treatment for the Mexican and Central American species of *Acer* is presented below. Each species is compared and contrasted with other sister taxa in a discussion section after each species group. Further analysis will be possible only after the taxonomic treatment of all North American maple species is completed, a task that has yet to be undertaken.

Taxonomic Treatment

Acer (Tourn.) L. 1753

Trees or shrubs mostly deciduous, up to 40 m high; opposite leaves, simple or imparipinnately compound, margin lobulate, crenate, or serrate; number of bud scales varies from 2 to 9–13 pairs; inflorescences terminal or lateral, corymbose, racemose, paniculate; flowers with 4–5 sepals, sometimes connate, 4–5 petals or apetalous, 8 stamens or 5, 10, or 12 stamens, nectary disc absent, intrastaminal or extrastaminal; pollen colpate or colporate; ovary bicarpellate or 3, 4, 5, 8 carpellate, two ovules per carpel; style branches estigmatic; schizocarpic fruits, indehiscent, with divergent or parallel wings; solitary seeds.

Key to the Mexican and Central American taxa of *Acer*

1. Leaves compound 2
   2. Leaves imparipinnate, 3–5 foliolate, flowers apetalous. 3
   2. Leaves mostly trifoliate, flowers petalous; Chihuahua . . . . ***A. glabrum* var. *neomexicanum***
      3. Petiolules absent or less than 1.6 cm long; northeastern Mexico 4
      3. Leaves 3–5 foliolate, leaflets dark green, ovate to widely ovate, margin serrate in upper half, petiolules absent or 0.1–2.8 cm; Mexico, Guatemala, Honduras. . ***A. negundo* subsp. *mexicanum***
         4. Leaves 3–5 foliolate, leaflets dull green, obovate to ovate, margin coarsely serrate along the upper half, petiolules absent or 0.1–0.8 mm; Nuevo León . . . . ***A. negundo* var. *texanum***
         4. Leaves 3-foliolate, leaflets pale green, oblong to ovate-rhombic, margin coarsely serrate to crenate, petiolules absent or 0.3–1.6 cm; Coahuila. . . . . ***A. negundo* var. *arizonicum***
1. Leaves simple 5
   5. Leaf width 3.5–11.1 cm, intersinus length 1–3.5 cm; northern Mexico 6
   5. Leaf width 6–24 cm, intersinus length 2.1–8.2 cm; Guatemala, Mexico (Chiapas, Guerrero, Jalisco, Tamaulipas) 7
      6. Leaves 4.2–11.1 × 3.7–13.9 cm, lobe projections often with large blunt teeth, rounded or obtuse, style 0.2–1.3 mm, stigma 2.3–7.4 mm; Chihuahua, Sonora . . . . ***A. grandidentatum***
      6. Leaves 3.5–9.5 × 3.6–11.8 cm, lobe with a few projections around the margin, rounded, style 0.5–2 mm, stigma 1.3–5.4 mm; Coahuila, Nuevo León, Tamaulipas . . . . ***A. grandidentatum* var. *sinuosum***
         7. Perianth 1.9–3 × 1.3–2.9 mm, stamen filament lenght 1.4–3.5 mm, wing sulcus 0.3–0.6 mm; Guatemala, Mexico (Chiapas, Tamaulipas) . . . . ***A. skutchii***
         7. Perianth 2.7–3.5 × 2.5–3.6 mm, stamen filament length 3.5–5.8 mm, wing sulcus 0.6–1.1 mm; Guerrero, Jalisco . . . . ***A. binzayedii***

Acer negundo subsp. ***mexicanum*** (DC.) Wesm., Bull. Soc. Roy. Bot. Belgique 29:43. 1890. *Negundo mexicanum* DC., Prodr. 1:596. 1824. *Acer serratum* Pax Bot., Jahrb. Syst. 6:296. 1885. *Acer mexicanum* (DC.) Pax, Bot. Jahrb. Syst. 7:212. 1886. *Acer negundo* var. *mexicanum* (DC.) Kuntze, Revis. Gen. 1:146. 1891. *Rulac mexicana* (DC.) Nieuwl., Amer. Midl. Nat. 2:140. 1911. *Negundo orizabense* Rydb., Bull. Torrey Bot. Club. 40:55. 1913. *Acer orizabensis* (Rybd.) Standley, Contr. U.S. Natl. Herb. 23:690. 1923. *Acer negundo* var.

FIG. 1. Morphological variation of *Acer negundo* subsp. *mexicanum* (DC.) Wesm. (A) Leaflets ovate to widely ovate, margin serrate, petiolules absent or 0.1–2.8 cm; (B, D) new inflorescence observed in May; (C) pollen grain oblate spheroid, exine rugulose.

orizabense (Rydb.) Standley & Steyerm, Field Mus. Nat. Hist. Bot. Ser. 23:60. 1944. *Acer negundo* subsp. *mexicanum* (DC.) Wesmael f. *glabrescens* E. Murray, Kalmia 8:17. 1978.

Tree 3–23 m tall, stem 15–45 cm in diameter; bark gray, fissured in older trees. *Petioles* purplish, tomentose or glabrous, 6.9–10.5 cm long; buds valvate. *Leaves* imparipinnate, 3–5 foliolate; leaflets ovate to widely ovate, acuminate at the apex, oblique or rounded at the base, margin serrate in upper half, adaxial side pilose or lanuginous, 4.7–16.8 × 1.9–11 cm; petiolules sessile or 0.1–2.8 cm. *Flowers* apetalous, unisexual (plants dioecious). *Perianth* sepals sparsely pubescent, reddish along edges, sepals 4, 0.6–1.6 × 0.6–0.9 mm. *Stamens* 4–6, filaments 1.3–2.5 mm long, anthers 3–4.7 × 0.6–1.1 mm, narrowly oblong, insertion basifixed, crimson when young, with trichomes, distal connective protrusion prominent cuspidate or caudate 0.2–0.6 mm in length; pollen tricolpate, oblate spheroid, 3 furrows, exine rugulose, with coarse reticulum, polar axis 20–41.5 µm, equatorial diameter 18.6–28.3 µm. *Pistil* with style 0.2–0.5 mm, nectary disc absent, stigma 5–8.4 mm. *Nutlet* flattened, spindle-shaped to rounded, sparsely pubescent, 0.7–1.8 × 0.3–0.9 cm, nutlet contact scar 0.3–0.6 cm; *wings* divergent at angle of 21°–60°, sparsely villous, wings 0.9–3.1 × 0.6–1.3 cm, wing sulcus 0.2–0.7 cm wide (Fig. 1).

Distribution and Ecology. This is the most widely distributed maple in the American tropics. In Mexico, it is present in 11 states. Eastern Mexico: San Luis Potosí (two municipalities), Puebla (three), Tlaxcala (one), Veracruz (seven). Central Mexico: Ciudad de Mexico (two municipalities), Estado de Mexico (two), Hidalgo (four). Western Mexico: Jalisco (two municipalities), Michoacán (nine), Oaxaca (two). Southern Mexico: Chiapas (two municipalities). Guatemala: 11 departments: Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, El Progreso, Quezaltenango, El Quiché, San Marcos, Sololá, and Totonicapán. Honduras: two departments: Comayagua and La Paz (Fig. 2). Elevation ranges from 1,200 to 2,700 m; however, a population in central Mexico reaches up to 3,200 m. Growing on clay or alluvial soils, sometimes on rocky substrates, along streams, pastures, or deep ravines, pine-oak forests or cloud forests. Associated taxa include *Abies* spp. Mill., *Pinus patula* Schltdl. & Cham. (Pinaceae), *Alnus acuminata* Kunth subsp. *arguta* (Schltdl.) Furlow, *Alnus jorullensis* Benth., *Alnus arguta* Spach, *Clethra* sp. L., *Ostrya* sp. Scop. (Betulaceae), *Cornus disciflora* Moc. & Sessé ex DC., *Cornus excelsa* Kunth (Cornaceae), *Fraxinus* spp. L. (Oleaceae), *Liquidambar styraciflua* L. (Altingiaceae), *Platanus lindeniana* M.Martens & Galeotti (Platanaceae), *Podocarpus* spp. L'Hér. ex Pers. (Podocarpaceae), *Prunus* spp. L. (Rosaceae), *Quercus* spp. L. (Fagaceae), *Salix bonplandiana* Kunth (Salicaceae), and *Tilia* spp. L. (Malvaceae).

Phenology. Flowering from December to March and fruiting from April to November. Leaves drying up and falling in November, but no autumnal coloration.

Common Names. Guatemala: ceibillo, raxoth ó raxoch ó Rax O'x (Alta Verapaz), granado (Baja Verapaz). Honduras: duraznillo, palomilla. Mexico: Amargoso, zarcillo (Michoacán), acezintle (Michoacán, Puebla), arce (Puebla), b. kantelates,

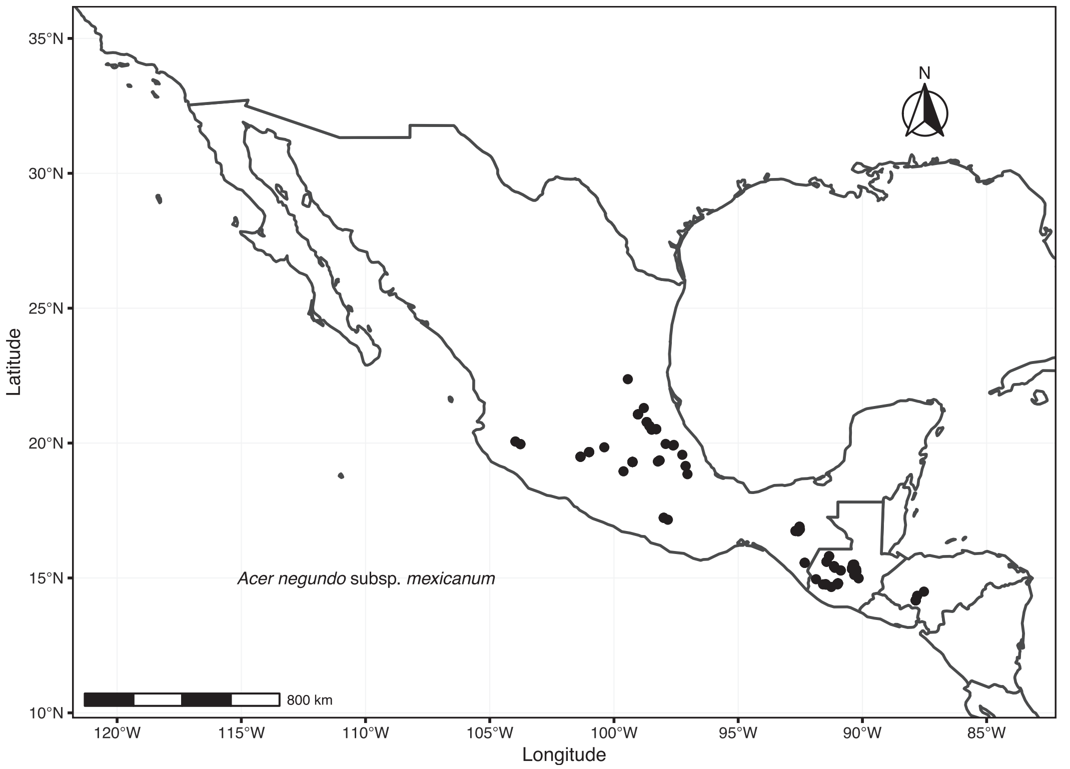

FIG. 2. Distribution of *Acer negundo* subsp. *mexicanum* (DC.) Wesm. Black dots represent populations.

icoj (Chiapas), palo blanco (Veracruz), zapoxihuil (Tlaxcala), zilozochitl (Hidalgo).

Uses. In hedgerows; prevention of soil drifting; branches used in Christmas nativities; leaves used as substrate for avocado seed germination.

Conservation Status. Species evaluted as vulnerable, VU B1ab(ii,iii,iv,v), under International Union for Conservation of Nature (IUCN) Red List guidelines (Vargas-Rodriguez 2011, IUCN 2012). Populations have low abundance, with scattered individuals in most of the populations. Deforestation and habitat fragmentation is common. Population in Jalisco State is almost extinct.

Specimens Examined. **GUATEMALA. Alta Verapaz:** Along Río Chió about 2–4 km southwest of Cobán, 1,300 to 1,400 m, 31 Jan–8 Feb 1969, *L.O. Williams et al. 40355, 40364* (BM, EAP, F, GH, MO, US, WIS); Cobán, 1,310 m, Feb–Mar 1886, *H. von Tüerckheim s.n*. (GH, K, US), 1,350 m, Feb–Mar 1907, *H. von Tüerckheim s.n*. (EAP, BM, F, GH, MO, NY), Jan 1978, *H. von Tüerckheim 19* (BM, P); 1–8 km northwest of Cobán, 1,200 to 1,300 m, 4 Jan 1973, *L.O. Williams et al. 42035* (EAP, F, MICH, US); Rio Cobán, about 5 km southeast of Tactic, 1,300 to 1,500 m, 5–7 Feb 1969, *L.O. Williams et al. 40698* (F, NY); near Cobán, 1,260 to 1,440 m, 26 Mar–15 Apr 1939, *P.C. Standley 69242* (A, F); Rio Frío entre Tactic y Santa Cruz, 1,450 m, 14 May 1963, *A. Molina & A.R. Molina 12243* (EAP, F, LL TEX, NY, US); NO de Tactic, 6 km a Estor, 1,500 m, 15 May 1963, *A. Molina & A.R. Molina 12290* (EAP, F, NY, US); vicinity of Cobán, 1,300 m, 23 Mar–19 Apr 1941, *P.C. Standley 90854* (F); along rio Carchá, between Cobán and San Pedro Carchá, 1,360 m, 26–27 Mar 1941, *P.C. Standley 90018* (F); 14 km east of San Pedro Carchá, 24 May 1971, *R.L. Wilbur 14880* (MICH); Cobán, 27 May 1904, *O.F. Cook & C.B. Doyle 210* (US), 1,310 m, 16 Feb 1941, *F.W. Hunnewell 17166* (GH); 193 km de la carretera hacia Cobán, 18 Mar 1990, *J.J. Castillo 1020* (AGUAT, MO, NY); above Santa Cruz, 1,380 m, 9 Apr 1939, *P.C. Standley 71012* (F); San Cristobal, 1,500 m, 28 Jul 1994, *O. et al. 94.3934* (BIGUA, USCG); 1 km después a San Cristóbal, carretera a Cobán, 1,500 m, 6 Jun 1997, *M. Véliz 97.6016* (BIGUA, USCG); **Baja Vera-**

paz: near Salamá, Jun 1904, *O.F. Cook 215* (US); Purulhá, Dec 1906–Jan 1907, *H. Pittier 166* (NY, US); below Pantín, 1,575 m, 4 Apr 1941, *P.C. Standley 91008* (F); region of Patal, 1,600 m, 30 Mar 1939, *P.C. Standley 69561* (F); Rio Santa Catarina near Santa Catarina in municipality San Jerónimo, 1,463 m, 24 Feb 1945, *A.J. Sharp 45259* (EAP, F, TENN); finca Los Cimientos, San Jerónimo, 1,800 m, 19 Apr 2001, *J. Meier 44* (BIGUA); **Chimaltenango:** Chichavac, 2,400 to 2,700 m, 18 Feb 1933, *A.F. Skutch 266* (US), 7 Jul 1933, *A.F. Skutch 350* (A, F, MICH, US); Tecpán, 2,194 m, 29 Jan 1945, *A.J. Sharp 4545* (F, MEXU, TENN); cerro de Tecpán, region of Santa Elena, 2,700 m, 4 Dec 1938, *P.C. Standley 58762* (A, F); **Guatemala:** 14.5 km Puerta Parada Sta. Catarina Pinul, 11 Mar 1992, *M. Dix 1344* (UVAL); **Huehuetenango:** 5 km northwest of Santa Cruz Barillas along road to San Mateo Ixtatán, 1,828 m, 7 Aug 1965, *D.E. Breedlove 11658* (F, LL TEX, MICH); between Barillas and Quetzal, 1,600 to 2,100 m, 30 Jul 1942, *J.A. Steyermark 49767* (A, F); between Paquix and Todos Santos, 2,470 m, 25 Sep 1944, *I.E. Melhus & G.J. Goodman 3567* (F); San Juan Ixcoy, rio San Juan, 2,000 m, 28 Mar 1995, *M. Véliz 95.4530* (AGUAT, BIGU, MEXU, USCG), 15 Feb 2005, *M. Véliz & R. Morales 15666, 15667* (BIGU); **El Progreso:** between Finca Piamonte and top of montaña Piamonte, along Joya Pacayal, 2,500 to 3,000 m, 7 Feb 1942, *J.A. Steyermark 43637* (A, F, NY); **Quezaltenango:** region of Azufral, northern slope of Volcán de Zunil, 2,300 to 2,500 m, 3 Feb 1941, *P.C. Standley 85753* (F); Volcán Santo Tomás, 3,000 to 3,300 m, 24 Jan 1940, *J.A. Steyermark 34955* (F); 1.6 km from base Santa Maria volcano, 2,438 m, 28 Dec 1963, *W.A. Eggler 437* (F); mountains southeast of Palestina, 2,700 m, 22 Feb 1939, *P.C. Standley 66057, 66369* (A, F, MICH, NY); Volcán Santa María, between Santa María de Jesús, Las Mojadas, 1,500 to 3,000 m, 12 Jan 1940, *J.A. Steyermark 33996* (F); between Fuentes Georginas and Zunil, 2,500 m, 4 Mar 1939, *P.C. Standley 67333* (F); aldea Chuimucubal, 2,710 m, 21 Dec 2004, *T.S. Quedensley 1822* (BIGU), 2,400 m, 3 Jan 2006, *T.S. Quedensley 2790* (BIGU); mirador del Santiaguito, 2,409 m, 12 Feb 2006, *M. Véliz et al. 16712* (BIGU); **El Quiché:** rio Juarco below Nebaj, 1,706 m, 6 Feb 1945, *A.J. Sharp 45105* (F, TENN); Nebaj, 2,194 m, 10 Dec 1934, *A.F. Skutch 1893* (A), May 1892, *Heyde & Lux 3278* (GH, MO, NY, P, US), 1,828 m, 28 Jun 1964, 25 Jun–17 Aug 1964, *G.R. Proctor 24961* (F, LL TEX), 1,889 m, 15 Nov 1934, *A.F. Skutch 1665* (A, F); Nebaj, about 500 m SE, on Sacapulas road, 6 Jun 1964, *E. Contreras 4896* (F, LL TEX); NW 1.6 km of Nebaj, 1,828 m, 4 Aug 1964, *B. Spross 89* (F); San Francisco, Cotzal, 3,700 m, 5 Dec 1934, *A.F. Skutch 1842* (A); Nebaj, 2,379 m, 12 Feb 2008, *M. Véliz & L. Velasquez 19737* (BIGU); Nebaj, 1,730 m, 29 May 2010, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1487, 1487b* (LSU); Chajul, 1,400 m, 5 Feb 2008, *E. Tribouillier s.n*. (BIGU); aldea Pulay, 317 km, 1,456 m, 12 Feb 2008, *M. Véliz et al. 19765, 19766* (BIGU); **San Marcos:** Puente de Nahuatl-aa near San Marcos, 2,280 m, 22 Feb 1939, *P.C. Standley 66245* (F); San Marcos, 2,480 m, 28 Apr 1946, *J.E. Maldonado 467* (USCG); **Sololá:** Volcán San Pedro, 20 Mar 2004, *A.L. MacVean s.n*. (UVAL); **Totonicapán:** Inter-American highway near Pologua, 2,700 m, 15 Jan 1965, *K. Lems s.n*. (NY, US);

HONDURAS. Comayagua: Montaña Zancudal, Oct 1979, *Catastro Forestal s.n*. (EAP); San José del Playón, 1979, *N. Agudelo 260* (HEH); **La Paz:** Ingrula, 1,950 m, 6 May 1986, *R. Felber 122, 123* (TEFH, HEH, EAP);

MEXICO. Unknown locality: *J. Cuatrecasas 3800* (F); Orizaba, 1,853 and 1,855, *F. Müller s.n*. (type: NY); **Chiapas.** St. Bartolo, *M. Linden s.n*. (P); beside small lake called Ik ‘al Nab near boundary of the municipios Zinacantán and Chamula along the trail from San Cristóbal las Casas to Zinacantán center, 2,377 m, 11 Mar 1965, *D.E. Breedlove 9277* (LL TEX), 21 Sep 1965, *D.E. Breedlove 12377* (MEXU); Chiapas, 1864–1870, *Ghiesbreght 807* (BM, GH, MO, NY); **Chamula municipality:** a orilla del rio Magdalena paraje Palan Chen, 1,650 m, 4 Aug 1983, *J.G. Garcia 601* (IBUG, MEXU, XAL); **San Andrés Larráinzar municipality:** ejido Santiago, 8 km al N de Larráinzar, 1,650 m, 22 Aug 1977, *J.I. Calzada et al. 3496* (MEXU); **San Cristóbal de las Casas municipality:** San Cristobal, Feb 1855, *M. Botteri 1379* (P), 2,164 m, 3 Mar 1965, *D.E. Breedlove 9201, 9204* (BM, F, LL TEX, MEXU, MICH, WIS), 12 Apr 1945, *E.J. Alexander 1051* (MEXU, MICH, NY); alrededores de San Cristobal, 18 Apr 1943, *F. Miranda 2652* (MEXU); arroyo Las Piedrecitas, 1 Apr 1985, *A.S. Ton 8137* (F, MEXU, MO); Santa Cruz en San Filipe, 15 Nov 1986, *A. Mendez Ton, 9782, 9834* (GH, LL TEX, MEXU, MO, NY); northeast edge of San Cristóbal Las Casas, 2,250 m, 20 Sep 1981, *D.E. Breedlove*

52958 (MO, MEXU); Cerro Huitepec, 16 Apr 2003, *Y.L. Vargas-Rodriguez 1718–1720* (LSU); **Siltepec municipality:** Siltepec, 2 Jan 1937, *E. Matuda 407* (MEXU, MICH, MO, US); **Tenejapa municipality:** El Arcotete, camino a Tenejapa, 2,300 m, 25 Mar 1983, *J.G. Garcia 563* (IBUG, MO, XAL); La Cueva yashanal, 15 Mar 1984, *A.S. Ton 7414* (F, IBUG, LL TEX, MO, WIS); 'Ach'lum, 2,773 m, 15 May 1967, *A.S. Ton 2304* (LL TEX, NY); Tenejapa center, 2,316 m, 7 Aug 1964, *D.E. Breedlove 6977* (BM, GH, F, MICH, NY); paraje of Balum K'anal, 2,407 m, 16 Mar 1965, *D.E. Breedlove 9358* (F, LL TEX, MICH); 700 m adelante de Balún Canán, camino San Cristóbal-Tenejapa, 2,100 m, 29 Apr 1993, *S. Ochoa-Gaona & N. Ramírez-Marcial 4089* (XAL); barrio of Banabil, paraje of Matsab, 2,682 m, 26 Aug 1966, *D.E. Breedlove 15354* (LL TEX, MEXU, MICH, NY); Cañada Grande, 8 Aug 2008, *Y.L. Vargas-Rodriguez 797* (LSU); **La Trinitaria municipality:** Boqueron, near Motozintla, 2,450 m, 4 May 1945, *E. Matuda 5364* (EAP, F, LL TEX, MO, NY); **Zinacantán municipality:** northwest side of Muk'ta vits (cerro Huitepec), 2,743 m, 18 Feb 1966, *R.M. Laughlin 154* (LL TEX, MEXU, NY); **Ciudad de México.** El Rosario, 20 Aug 1936, *L.H. MacDaniels 638* (F); **Álvaro Obregón municipality:** environs de San Angel dans les Pedregales, *Schnée s.n.* (MICH, P); **Magdalena Contreras municipality:** Cañada de Contreras, cerca del Segundo Dinamo, 2,700 m, 20 Feb 1966, *J. Rzedowski 21967, 21968* (LL TEX, MICH), 8 Mar 1964, *J. Rzedowski 18272* (LL TEX, MICH); Cañada de Contreras, entre el Primero y Segundo Dinamo, 2,600 m, 9 Mar 1975, *J. Rzedowski 32774, 32775* (F, NY); Cañada Contreras, Jan 1912, *C. Reiche s.n.* (MEXU); Contreras, 26 Jul 1941, *P.L. Lyonnet 3263* (US); rio de la Magdalena, between Contreras and the second dynamo, 2,590 m, 23 Jul 1944, *A.J. Sharp 4454* (GH, MEXU, NY, TENN); Segundo Dinamo en Contreras, 28 Jun 1964, *B.J. Páez 3* (LL TEX); Eslava, Apr 1938, *E. Lyonnet 2059* (US), *E. Lyonnet 2060* (MEXU, US); **Estado de México.** Rio Hondo, 2,286 to 2,438 m, 12 Feb 1899, *C.G. Pringle 7705* (F, GH, MEXU, MO, US); Ixtaccihuatl, 2,133 to 2,438 m, Mar–Jul 1903, *C.A. Purpus 218* (MO, US); **Amecameca municipality:** Cañon al E de Santiago Cuautenco, 2,650 m, 1 Mar 1969, *J. Rzedowski 26708* (ARIZ, WIS); Cerro de Venacho, 3,200 m, 15 Feb 1953, *E. Matuda 32233* (MEXU); **Coatepec Harinas municipality:** Barranca de Texalotengo at Rancho Santo Tobias near Villa Guerrero, 25 Feb 1943, *C.L. Gilly & R.F. Simpson 11* (MICH, NY, TENN); **Hidalgo. Chapulhuacán municipality:** Km 296, Mexico City–Laredo highway, between Jacala and Chapulhuacan, 6,000 ft, 12 Jul 1943, *C.L. Lundell 12217* (LL TEX, MICH, NY, US); **Molango de Escamilla municipality:** Rio Malila, 6 km al sur con referencia a Molango, 1,600 m, 22 Apr 1992, *J.L. López 281* (IBUG, IEB, MEXU); Xochicoatlán, 13 Sep 1964, *L. González 1564* (WIS); **Xochicoatlán municipality:** 1 km al N de Xochicoatlán, 2,100 m, 5 Mar 1982, *P. Tenorio & R. Hernández 142* (ARIZ, LL TEX, MEXU); **Zacualtipán municipality:** Tlatoxca, 7 km al SE de Zacualtipán, 1,755 m, 12 Jan 1993, *J.L. López 512* (IBUG, IEB, MEXU); rio Panotlan between Zacualtipan and Olotla on road to Metztitlan, 1,600 to 2,000 m, 21 Mar 1947, *H.E. Moore Jr. 2384* (GH); Cumbre de Tlahuelompa, 7 km del entronque de la carretera federal Zacualtipán-Metzquititlán, 13 Jun 1992, *J.L. López 95* (IBUG, IEB); Tlahuelompa, 3.5 km al SE, camino a Tzincoatlán, 1,830 m, 17 Aug 1995, *O. Alcántara 2309* (MEXU); **Jalisco. Gómez Farías municipality:** 12 km an N de Ferrería, brecha a la Cofradía, 1,880 m, 23 Sep 1990, *J. Villa et al. 905* (IBUG, IEB); **Tapalpa municipality:** Orilla S de Tapalpa por el arroyo, junto al puente de la brecha a Venustiano Carranza, 2,000 m, 12 Mar 1989, *A. Flores et al. 1516* (IBUG, WIS); junto al rio, 2 km al N del pueblo, 1,950 m, 17 Jun 1989, *A. Buenrostro 8* (IEB), *C. Garcia 9* (IBUG); orilla de rio Tapalpa al noroeste del pueblo 2.5 km, 17 Jun 1989, *C. Ortiz 2* (IBUG); Tapalpa, 2,200 m, 18 May 1970, *C.L. Díaz 1674* (IBUG, MICH); Puente Grande, 31 Oct 2015, *Y.L. Vargas-Rodriguez et al. 1820, 1821* (LSU), 14 May 2016, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1845* (LSU), 25 Sep 2016, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1851* (LSU); Presa del Nogal por camino a San Gabriel, 31 Oct 2015, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1822, 1823* (LSU); Atacco, 14 May 2016, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1846* (LSU); **Michoacán.** Ruta 15 Zitácuaro a Morelia, Mil Cumbres, 2,500 m, 16–17 Jan 1982, *J. Miller & R. Cedillo 3790* (F, MEXU, MO); Cerca del Puerto Mil Cumbres, km 240 de la carretera México-Morelia, 2,350 m, 20 Jul 1964, *J. Rzedowski 18359* (LL TEX, MEXU, MICH); 6 km de la desviación a Aporo al NW de Angangueo, 2,325 m, 27 Apr 1982, *R. Torres & E.*

Martínez 319 (MICH, MO); **Acuitzio municipality:** Al NO de Acuitzio del Canje, 2,100 m, 3 Apr 1986, *H. Díaz 2156, 2157* (IBUG, MEXU, XAL); **Angangueo municipality:** Rondanilla, 2,300 m, 27 May 1988, *X. Madrigal 4274* (IEB, MEXU, MO, XAL); **Charo municipality:** "Campo por Turistas" 23 km east of Morelia on highway 15 (at km 291), 2,300 m, 22 Jul 1960, *H.H. Iltis et al. 358* (MICH, MEXU, WIS, US); **Hidalgo municipality:** along a mountain stream 16 km west of Ciudad Hidalgo, 2,300 to 2,500 m, 28 Oct 1960, *R. McVaugh et al. 20474* (MICH); **Maravatío municipality:** Palo Seco, aprox. 6 km carretera Maravatío-Tlalpujahua, 2,000 m, 16 Mar 1991, *E. Pérez & E. García 2095, 2096* (IEB, XAL); **Morelia municipality:** Monterubio, 2,050 m, 13 Apr 1989, *J.M. Escobedo 1766* (IBUG, IEB, MEXU, XAL); Ha. Quinceo, 1,900 m, 1 Apr 1909, *G. Arsène 2024* (12024?) (MEXU), 21–25 May 1909, *G. Arsène 3027* (F, GH, MEXU, MO, P, US); Rio Grande, 1,850 m, 1 Nov 1910, *G. Arsène 5684* (GH, MEXU, MO, US), 1,900 m, 6 Jun 1912, *G. Arsène 8332* (NY, P); Cerro Azul, 3 Jan, *G. Arsène s.n.* (F); Cañada del Rio Grande, cerca de Cointzio, 1,950 m, 9 Jul 1987, *J. Rzedowski 43595* (IEB); **Salvador Escalante municipality:** Copándaro, 2,200 m, 6 Mar 1986, *J.M. Escobedo 862, 863* (IBUG, IEB); **Tuxpan municipality:** Cañada del Puerto de la Cantera, 8.7 km al O de Tuxpan, carretera a Cd. Hidalgo, 1,780 m, 1 Nov 1984, *R. Torres & M. Ramírez 13506* (IEB, XAL)**; Oaxaca.** Near Chicahuaxtla, about 35 km southwest of Tlaxiaco, 2,400 m, 7 Feb 1965, *R. McVaugh 22317* (MICH); Santa Maria Asunción, a 10 km al SE de Juxtlahuaca, 1,600 m, 19 Aug 1976, *M. Souza et al. 5815* (MO); **Putla Villa de Guerrero municipality:** Cerro Zarzamora, San Andres Chicahuaxtla between Nochixtlan and Putla, 28 Jan 1968, *M.C. Carlson & T. MacDougall 3936* (F); **Santiago Juxtlahuaca municipality:** Santa María Asunción, 14 km al SW de Juxtlahuaca, Cerro de la Campana, 1,750 m, 4 Apr 1982, *P. Tenorio & R. Torres 169* (MO, XAL); **Puebla.** Rio Atoyac, 21 Mar 1914, *A. Gineste s.n.* (MEXU); Hacienda Cristo, 28 Aug 1909, *H. Nicolas s.n.* (P); Mayorazgos, 19 Sep 1911, *H. Nicolas 6124* (P); Camino a Apulco, 21 May 1968, *W. Boege 760* (GH); **Puebla municipality:** vicinity of Puebla, 2,120 m, 4 Jul 1907, *G. Arsène 1342* (MO, US); Santa Barbara près Puebla, 20 Jul 1910, *H. Nicolas s.n.* (NY, P); **Zacapoaxtla municipality:** Cascada de La Gloria, cerca de Apulco, 1,400 m, 12 Apr 1974, *J. Rzedowski 31870* (MICH); Apulco, 15 Mar 1970, *W. Boege 1346* (MEXU); Cascada de La Gloria, cerca de Apulco, 1,400 m, 12 Apr 1974, *J. Rzedowski 31870* (ARIZ, EAP, LL TEX); **Zacatlán municipality:** Zacatlán, 3 Apr 1913, *F. Salazar s.n.* (US); **San Luis Potosí.** Prov. de San Luis, 1851, *Virlet d'Aoust s.n.* (P); San Luis Potosí, 21 Mar 1987, *C.H. Ramos 33* (ARIZ, F, LL TEX, MEXU); **Cárdenas municipality:** Las Canoas, 26 Nov 1890, *C.G. Pringle 3652* (GH); **Ciudad del Maíz municipality:** 3 km south of Papagayos, 29 Apr 1950, *R.J. Newman 61* (US); **Tamasopo municipality:** Tamasopo Cañon, 26 Nov 1890, *C.G. Pringle 3652* (A); **Tamazunchale municipality:** Highway 85, 48 km north of Tamazunchale, 1,524 m, 24 Mar 1964, *D. Ahshapanek 233* (LL TEX); **Tlaxcala.** Santa Ana, 20 Jul 1910, *H. Nicolas 5271* (MEXU, US); Camino de Tlaxcala hacia San Juan Totolac, 2,230 m, 5 Mar 1989, *H. Vibrans 2611* (MEXU); **Amaxac de Guerrero municipality:** along rio Zuahuapan, near San Bernabé, 2,164 m, 20 Aug 1944, *A.J. Sharp & E. Hernández X. 44452* (GH, NY, MO, TENN); near Santa Cruz, 20 Aug 1944, *E. Hernández X. 345* (LL TEX); **Veracruz. Altotonga municipality:** on highway 131, 21 km from junction with highway 141, 1,500 m, 29 Apr 1986, *J.V. LaFrankie 1083* (GH, TENN); **Calcahualco municipality:** Orillas riachuelo por Atotonilco, 1,950 m, Feb 1982, *M. Cházaro & H. Oliva 2100* (MEXU); Excola, camino a San Francisco, 1,700 m, 17 Mar 1986, *J.L. Martinez & J.L. Garcia 1147* (IEB, XAL); **Chiconquiaco municipality:** Planta del Pie, 1,960 m, 24 Mar 1972, *F. Ventura 5137* (MICH, LL TEX); **Huayacocotla municipality:** Camino a Rancho Nuevo, 2,000 m, 8 Mar 1972, *R. Hernandez 1541* (F); carr. Huayacocotla a Viborillas, 1 km de Huayacocotla, 2,300 m, 14 Jul 1977, *J.J. Fay & J.I. Calzada 905* (F, GH, LL TEX, NY, US, XAL); entre Viborillas y Huayacocotla, 28 Mar 1975, *V. Sosa 11* (F, NY, XAL); 2 km carretera Huayacocotla-Viborilla, 2,100 m, 31 Mar 1985, *L. Cabrera-Rodriguez 3* (MEXU, XAL); Huayacocotla, 2,170 m, 24 Abr 1971, *R. Hernandez & R. Cedillo 1160* (F, GH); 3 km southwest of Huayacocotla along road to Palo Bendito, 2,150 to 2,250 m, 22 Jul 1982, *M. Nee & G. Diggs 25199* (BM, F, WIS); 1 km east of Viborillas, 1,950 to 2,200 m, 26 Jan 1984, *M. Nee & K. Taylor 29057* (F, NY); **Orizaba municipality:** environs d' Orizaba, Feb 1855, *M. Botteri & A.L.J.F. Sumi-*

chrast 1379 (P); Orizaba, *M. Botteri 861* (GH, US); Orizaba, Jul 1855 (1856?), *M. Botteri 1062* (BM, GH, K, P); Veracruz to Orizaba, 1857, *F. Mueller 1373* (K); **Perote municipality:** Colonia Justo Sierra, carretera para el Cofre de Perote, 2,500 m, 27 Abr 1982, *J.I. Calzada 8702* (XAL); **Vigas de Ramírez municipality:** La Joya, 2,000 m, Apr 1982, *M. Cházaro & H. Oliva 2250* (LL TEX, MEXU, XAL).

Acer negundo var. ***arizonicum*** Sarg., Bot. Gaz. 67:240. 1919.

Small tree 8–12 m tall; bark light gray. *Petioles* green, glabrous, slender, 4.5–9.5 cm long; buds valvate. *Leaves* imparipinnate, trifoliolate; leaflets pale green, sometimes with 2 lobes, oblong to ovate-rhombic, acute or acuminate at the apex, cuneate sometimes oblique at the base, margin coarsely serrate to crenate, adaxial side with tufts of axillary lanuginous hair, 9.6–13.5 × 4.1–6.5 cm; petiolules sessile or 0.3–1.6 cm. *Flowers* not seen. *Nutlet* not seen in specimens from Mexico; *infructescence* racemes glabrous, 8–10 cm in length, fruit spreading, glabrous, not constricted at the base according to holotype description (Fig. 3a).

Distribution and Ecology. North Mexico: Coahuila State. Along Sierra Maderas del Carmen. Found in two areas in Ocampo municipality (Fig. 4). Elevation ranges from 1,500 to 2,250 m. Present in steep canyons. Growing in gravelly and sandy loam soils derived from extrusive igneous rocks. Associated taxa: *Quercus* spp. (Fagaceae), *Pinus* spp. L., *Pseudotsuga* sp. Carrière (Pinaceae), *Tilia* sp. (Malvaceae), *Garrya* sp. Douglas ex Lindl. (Garryaceae), *Ceanothus* sp. L. (Rhamnaceae), *Fendlera* sp. Engelm. & A.Gray (Hydrangeaceae), *Fraxinus* sp. (Oleaceae), and *Rhus* sp. L. (Anacardiaceae).

The US populations of the taxon are located in Arizona and New Mexico.

Common Names. Not known (Mexico), Arizona boxelder (USA).

Conservation Status. The species is evaluted as Data Deficient (DD) under the IUCN Red List guidelines (IUCN 2012).

Specimens Examined. **MEXICO. Coahuila: Ocampo municipality:** Canyon Hundido on north side of Pico de Centinela, Sierra del Jardin, 8 km east of Rancho El Jardin by winding road, 1,500 to 2,250 m, 27 Jul 1973, *M.C. Johnston et al. 11769* (LL TEX); ca 32 km east-southeast of Boquillas in Sierra del Carmen, ca 4 km east of Rancho El Jardín in Canyon Hundido on the northernmost north-facing igneous canyon of the Sierra del Carmen, 2,100 m, 27 Jul 1973, *J. Henrickson 11448* (LL TEX).

Acer negundo var. ***texanum*** Pax, Bot. Jahrb. Syst. 7:212. 1886. *Rulac texana* (Pax) Small, Fl. SE U.S. 743. 1903. *Negundo texanum* (Pax) Rydb., Bull. Torrey Bot. Club 40:56. 1913. *Acer californicum* var. *texanum* Pax Bot. Jahrb. Syst. 11:75. 1890. *Negundo interius* subsp. *texanum* (Pax) Holub, Folia Geobot. Phytotax. 9:273. 1974. *Acer negundo* var. *latifolium* Pax Bot. Jahrb. Syst. 11:75. 1890. *Acer negundo* subsp. *latifolium* (Pax) Schwer. Gartenflora 42:205. 1893.

Small tree 4–15 m tall, stem 40–50 cm in diameter. *Petioles* pale pubescent or glabrous, 4–8 cm long; buds valvate. *Leaves* imparipinnate, 3–5 foliolate; leaflets obovate to ovate, acute at the apex, cuneate or rounded at the base, margin coarsely serrate along the upper half, adaxial side pilose sometimes with tufts of axillary hairs, 5.3–11.2 × 3.1–7.5 cm; petiolules sessile or 0.1–0.8 mm. *Flowers* apetalous, unisexual (plants dioecious). *Perianth* sepals sparsely pubescent, sepals 4, 1.1–1.4 cm long. *Stamens* 4–5, filaments 1.9–2 mm long, anthers 3.3–4.6 × 0.7–1 mm, narrowly oblong, greenish, trichomes absent, distal connective protrusion 0.3–0.4 mm. *Pistil* with nectary disc absent. *Nutlet* flattened, elongated sometimes slightly rounded, sparsely villous; 0.8–1 × 0.3– 0.9 cm, nutlet contact scar 0.35–0.4 cm; *wings* divergent at the angle of 16°–19°, wings 1.3–1.8 × 0.7–0.9 cm, wing sulcus 0.3–0.45 cm wide (Fig. 3b).

Distribution and Ecology. Northeastern Mexico: Nuevo León State (Fig. 5). Along a mountain in Santiago municipality. Elevation ranges from 750 to 1,500 m. Sandstones and sedimentary substrates present in the localities. Growing along streamsides in cloud forest. Associated taxa: *Pinus* sp. (Pinaceae), *Quercus* sp. (Fagaceae), *Juglans* sp. L. (Juglandaceae), *Platanus rzedowskii* Nixon & J.M.Poole (Platanaceae), *Populus tremuloides* Michx. (Salicaceae), *Colubrina greggii* S. Watson (Rhamnaceae).

The species is distributed in Kansas, Missouri, Oklahoma, and Texas in the USA.

Fig. 3. Morphological variation of (A) *Acer negundo* var. *arizonicum* Sarg.: leaflets pale green, oblong to ovate-rhombic, margin coarsely serrate to crenate, petiolules absent or 0.3–1.6 cm; (B) *Acer negundo* var. *texanum* Pax: leaflets obovate to ovate, margin coarsely serrate, petiolules absent or 0.1–0.8 mm.

Phenology. Fruits seen from April to September.

Common Names. Not known (Mexico), box-elder (USA).

Conservation Status. The species is evaluted as of Least Concern (LC) under the IUCN Red List guidelines (IUCN 2012). The species is widely distributed in the USA; however, it is only known from one locality in Mexico.

Specimens Examined. **MEXICO. Nuevo León: Santiago municipality:** mountains near Monterrey, Jul 1933, *C.H. Mueller & M.T. Mueller s.n.* (A, F, MEXU, LL TEX); 38 km (23 mi) south of Monterrey, on Pan American Highway (Horsetail Falls), 25 Apr 1939, *T.C. Frye & E.M. Frye 2465* (GH, MICH, MO, NY, US); near Horsetail Falls, 762 m, 3 Jul 1941, *W.C. Leavenworth & M. Leavenworth 806* (F); in woods along trail to Cola de Caballo, 4 Sep 1948, *G.L. Webster & D. Preston 2864* (LL TEX); ravine just below Horsetail Falls itself, Hacienda Vista Hermosa, above Cercado (40 km S of Monterrey), 792 m, 9 Jul 1953, *W.E. Manning & M.S. Manning 53196* (MEXU); cascada Cola de Caballo, 750 m, 7 May 1976, *M. Cházaro 502* (XAL); áreas cercanas a Cola de Caballo, 800 m, 20 Jul 1984, *J.A. Villarreal et al. 2762* (LL TEX); parque Cola de Caballo, 1500 m, 25 Jun 1987, *E. Estrada 1137* (MO); Hacienda Vista Hermosa, 56 km south of Monterrey, 762 m, 29 Jun 1939, *S.S. White 1638* (ARIZ, GH, MICH, US); paraje de Los Osos, al pte. de Yerbanís, 24 Jul 1964, *J. Marroquín 494* (LL TEX).

Discussion About the *A. negundo* Group. *Acer negundo* comprises four subspecies and one variety according to van Gelderen *et al*. (1994). The varieties or forms were established based on the color of samaras and the pubescence on leaves and branchlets, but the taxonomic status of some of them is not well supported (Sargent 1919, Murray 1975). Based on the morphological evidence, the subspecies status of *Acer negundo* subsp. *mexicanum* is maintained here, as proposed by van Gelderen *et al*. (1994). The subspecies

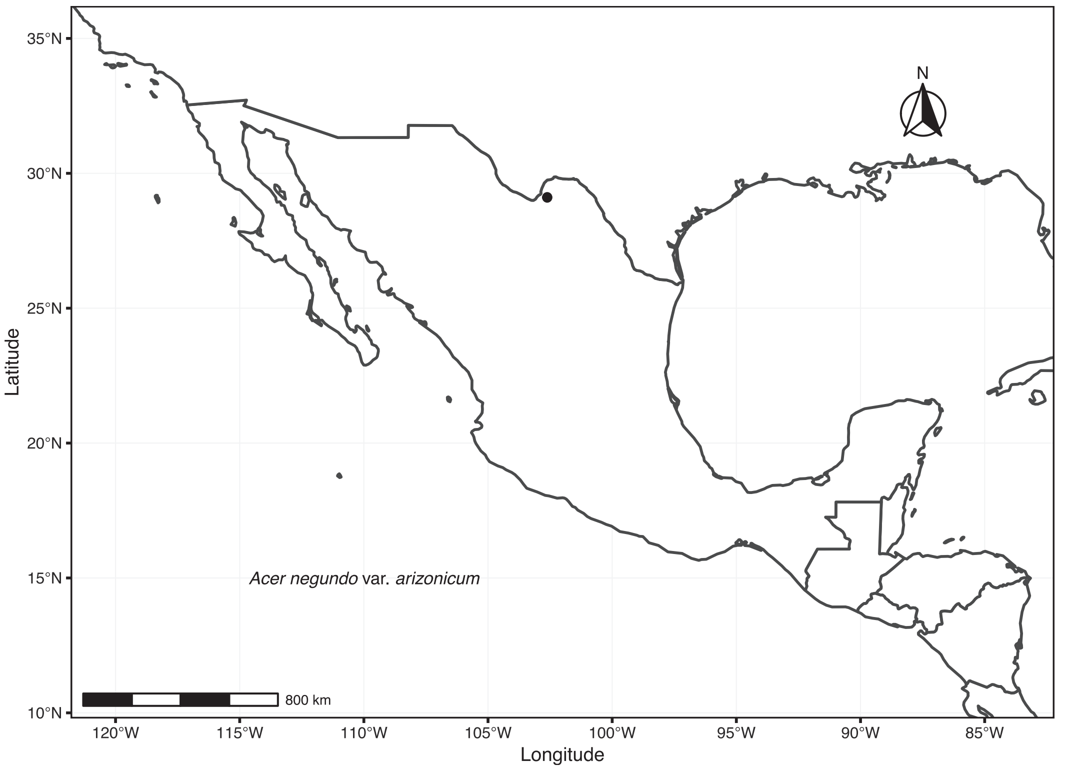

FIG. 4. Distribution of *Acer negundo* var. *arizonicum* Sarg. Black dots represent populations.

negundo is commonly found in northeastern USA and differs from the subspecies *mexicanum* by serrate leaflets and very wide nutlets. The variety *orizabense* is maintained as synonym, in agreement with the species descriptions in the regional floras of Mexico (Cabrera-Rodríguez 1985, Calderón de Rzedowski 2001). The variety *orizabense* was described from Mexico based on the sparse abaxial pubescence of the leaves, although the variety is not geographically isolated from the subspecies *mexicanum* and cannot be considered a separate entity based on the floral differences. Gibbs and Chen (2009) described a wide distribution for the subspecies *mexicanum*, with connected populations in central Mexico and throughout Guatemala. However, based on field observations, the populations are small, fragmented, and usually present as small patches along creeks in mountains of both Mexico and Guatemala. *Acer negundo* subsp. *mexicanum* with its populations in Honduras is the *Acer* species with the southernmost distribution on the American continent. The examination of herbarium material expanded the range of this taxon to Honduras.

Acer negundo var. *arizonicum* is treated as a synonym of *A. negundo* subsp. *californicum* in van Gelderen *et al.* (1994). However, the slender, long, glabrous petioles and glabrous fruit distinguish this variety proposed by Sargent (1919) from subspecies *californicum,* which is characterized by tomentose petioles and branchlets and pubescent fruit pedicels. Thus, here the populations in Coahuila, Mexico, are treated as the variety *arizonicum*. The variety *arizonicum* is characterized by oblong to ovate-rhombic leaflets with coarsely serrate to crenate margins, and petiolules sessile or 0.3–1.6 cm; it is only known from Coahuila. Subspecies *californicum* has stigmas 5.9–6.8 mm long (smaller than those in subspecies *mexicanum*) and nutlets 0.3–0.4 cm; it is documented for California.

Acer negundo var. *texanum* is considered by van Gelderen *et al*. (1994) as intermediate between the subspecies *negundo* and *californicum*. The present study distinguished variety *texanum* by its leaflets obovate to ovate, acute at the apex, with margins

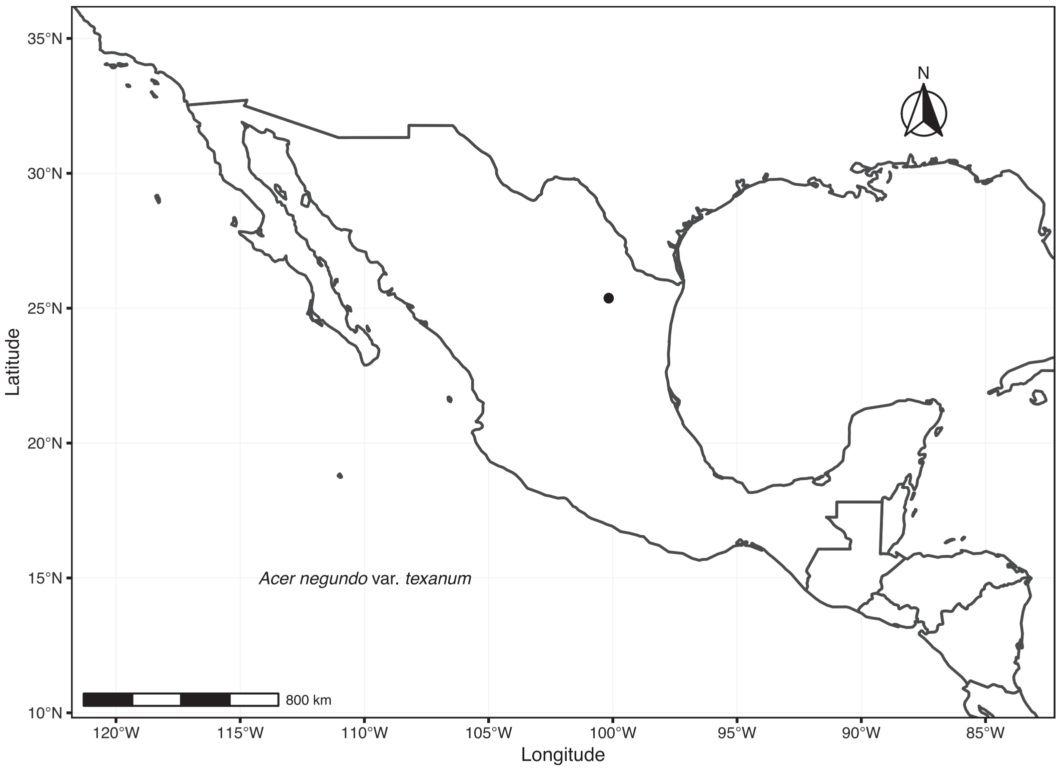

Fig. 5. Distribution of *Acer negundo* var. *texanum* Pax. Black dots represent populations.

coarsely serrate along the upper half, and petiolules sessile or 0.1–0.8 mm; the variety occurs in Texas, and the present work established its presence in Nuevo León, Mexico. The subspecies *mexicanum* differs from the variety *texanum* in the leaf margin and larger size of nutlets. The variety *interius* has lobed leaflets and a more irregularly serrate leaf margin compared with those in the variety *texanum*; it is distributed in the Rocky Mountains and the Great Plains.

Previous literature recognized only one subspecies of *A. negundo* in Middle America (*Acer negundo* subsp. *mexicanum*) (Murray 1980a, 1980b, van Gelderen *et al*. 1994). Here, the existence of three infraspecific entities in Mexico is documented: *A. negundo* subsp. *mexicanum*, *A. negundo* var. *arizonicum*, and *A. negundo* var. *texanum*. There is a record of *A. negundo* near Naco, Sierra de San José, Sonora (Mearns, in 1907), but the specimen was not seen and its infraspecific status could not be established.

Acer glabrum **var.** ***neomexicanum*** (Greene) Kearney & Peebles J. Wash. Acad. Sci. 29:486. 1939. *Acer glabrum* subsp. *neomexicanum* (Greene) A. E. Murray Kalmia 2:1. 1970. *Acer neomexicanum* Greene Pittonia 5:3. 1902.

Small tree 8–10 m tall, stem 10–40 cm in diameter, freely branching; bark smooth, dark grey. *Petioles* glabrous, reddish or grayish when mature; buds elongated, scales 2 to 4, paired, red, 2–3 mm long. *Leaves* usually 3-parted, or nearly so, rhombic or obovate, leaf base attenuate, margin coarsely serrate and occasionally doubly serrate, acute to acuminate at the apex, apical projection 0.6–1 cm long; lamina 5.4–7.5 × 5–7 cm, radius 0.5–2.5 cm, midvein 5.1–7.5 cm, main lateral vein 4–6.3 cm, intersinus 1.5–2.4 cm, abaxial and adaxial sides glabrous. *Flowers* in corymb, petalous, green to yellowish, unisexual (plants monoecious). *Perianth* 5–6 × 5–8.5 mm, sepals spatulate to oblong, twice as long as the petals. *Nutlet* glabrous, rugose, flat; 5–6 × 6 mm; distal keel slightly rounded, nutlet contact scar 6–7 mm; *wings* sometimes overlapping, divergence angle 16°–17°; wings 1.9–2.3 × 0.8–1.1 cm, wing sulcus 4–5 mm wide (Fig. 6).

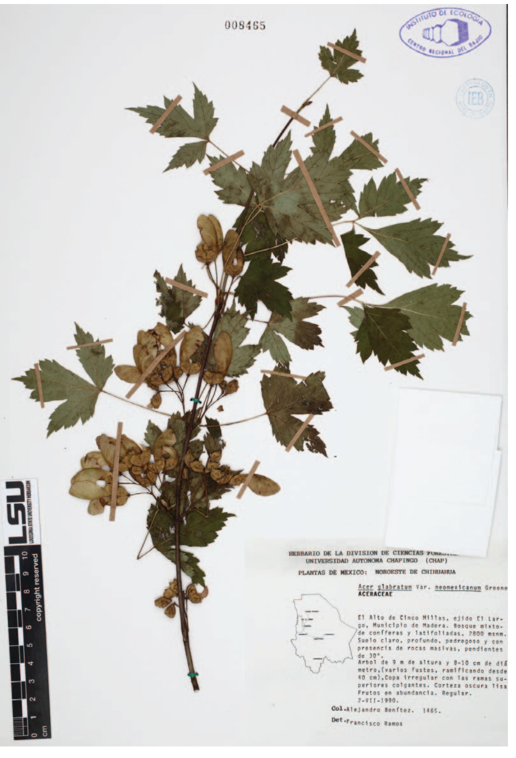

FIG. 6. Morphological variation of *Acer glabrum* var. *neomexicanum* (Greene) Kearney & Peebles; leaves trifoliate or nearly so, with margin serrate.

Distribution and Ecology. Northwestern Mexico: Chihuahua State (Fig. 7). Along Sierra Madre Occidental. Ocurring at two localities in Maderas municipality. Elevation ranges from 2,600 to 2,800 m. Growing on gravelly and rocky soils. Present in conifer and hardwood forests. Ocurring in ravines with steep slopes (30%–54%). Associated taxa are *Abies* sp.*,* *Pinus* sp. (Pinaceae), *Juniperus* sp. L. (Cupressaceae), and *Quercus* sp. (Fagaceae).

The species populations are also distributed in Arizona, Colorado, New Mexico, and Utah in the USA.

Phenology. Flowers seen in May and fruits in June and July.

Common Names. Not known (Mexico), New Mexico maple (USA).

Conservation Status. The species is evaluted as of Least Concern (LC) under the IUCN Red List guidelines (IUCN 2012). There is commercial wood extraction in the area of its distribution. The species has low abundance in Mexican localities.

Specimens Examined. **MEXICO. Chihuahua: Madera municipality:** El Alto de Cinco Millas, ejido El Largo, 2,800 m, 2 Jul 1990, *A. Benítez 1465* (IEB, MEXU); arroyo Las Garrochas, ejido El Largo, 2,600 m, 3 May 1992, *E. Guízar N. 2654* (IEB, MEXU); Sierra Cinco Millas, 11.1 km (by air) north-northwest of Madera, 2,639 m, 21 Jun 2012, *A.D. Flesch s.n*. (MABA database).

DISCUSSION ABOUT THE *A. GLABRUM* GROUP. *Acer glabrum* is a variable species from western North America. There are six infraspecific taxa growing in the American continent, *diffusum*, *douglasii*, *glabrum*, *greenei*, *neomexicanum*, and *torreyi*, all distinguished by leaf morphology (van Gelderen *et al*. 1994). In his systematic study, Justice (1995) reported that leaf morphology varied with climate and the variation was related to discrete geographical ranges. He concluded that, besides leaf variation, there were no conspicuous differences and therefore, the subspecies proposed by van Gelderen *et al*. (1994) deserved varietal status. The present work adopted the treatment proposed by Justice (1995) upon examination of the material.

Variety *neomexicanum* is present in Colorado, Utah, New Mexico, Arizona, and the neighboring Mexican state of Chihuahua. In contrast to other varieties, it produces mostly trifoliate leaves. Variety *diffusum* has small leaves, < 3 cm wide; variety *douglasii* has the widest leaves at 8–18 cm; while the other three varieties have leaves of intermediate size, but differ in having a moderate to deep sinus (variety *glabrum*), narrow and deep sinus (variety *torreyi*), and wide to very deep sinus (variety *neomexicanum*). Variety *greenei* from California is considered by some authors a nonvalid taxon (Justice 1995).

The examination of herbarium material established the presence of *A. glabrum* var. *neomexicanum* for the first time in northern Mexico, a record with no mention in the previous literature.

Acer grandidentatum Nutt. in Torr. & A. Gray Fl. N. Am. 1:247. 1838. *Acer brachypterum* Woot. & Standl. Contr. U. S. Nat. Herb. 16:146. 1913. *Acer saccharum* subsp. *brachypterum* (Wooton & Standley) E. Murray, Kalmia 7:15. 1975. *Acer saccharum* var. *grandidentatum* Sudw. Rep. Sec. Agr. 1892:325. 1893. *Acer saccharum*

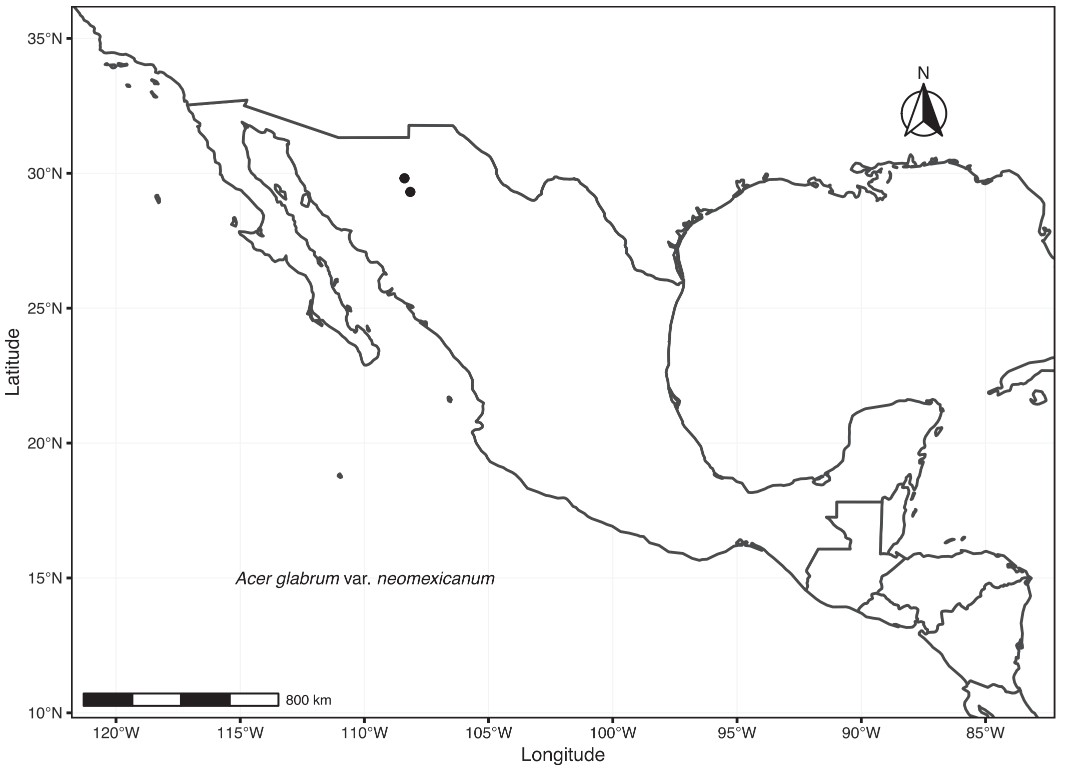

FIG. 7. Distribution of *Acer glabrum* var. *neomexicanum* (Greene) Kearney & Peebles. Black dots represent populations.

subsp. *grandidentatum* (Nutt.) Desmarais, Brittonia 7:383. 1952.

Tree 8–20 m tall, deciduous, stem 40–70 cm in diameter; bark dark grey, shallowly furrowed and flaky. *Petioles* tomentose or glabrous. *Leaves* with 5 lobes, leaf base cordate sometimes truncate or reniform, minor lobes overlapping, lobe projections often with large blunt teeth, rounded or obtuse; lamina 4.2–11.1 × 3.7–13.9 cm, midvein 3.9–10.7 cm, main lateral vein 3.3–10.2 cm, intersinus 1.2–3.5 cm, horizontal vein 1.5–9.4 cm, abaxial side tomentose. *Flowers* in corymbs, yellow, apetalous, unisexual (plants with labile sex expression). *Perianth* connate, with lobes, sparsely villous; perianth 2.3–4.1 × 1.7–4.5 mm. *Stamens* 5–10, filaments reddish, 3.7–6.1 mm long, the anthers 1.4–2.5 × 0.7–1.5 mm, elliptic, base rounded, attachment basifixed, and distal connective protrusion absent. *Pistil* with style 0.2–1.3 mm, nectary disc 0.4–0.8 mm high, stigma 2.3–7.4 mm; male flowers with abortive pistil pilose and stigma reddish. *Nutlet* elliptic, glabrous or sparsely pilose at the base, with reticulated veins, inflated; 0.6–0.9 × 0.5–0.8 (0.9) cm; distal keel absent or inconspicuous, nutlet contact scar 0.3–0.6 (0.7) cm; *wings* with coalescent proximal veins sparsely distributed, reticulate veinlets present; wings 1.1–2.1 (3.1) × 0.4–0.9 (1.8) cm, wing sulcus 0.3–0.7 cm wide (Fig. 8a).

Distribution and Ecology. Northwestern Mexico: Chihuahua and Sonora states (Fig. 9). Along Sierra Madre Occidental: in the western side of Chihuahua in Bocoyna, Casas Grandes, Guachochi, Madera, Ocampo, and Temósachic municipalities. Present in Barranca del Cobre and the protected areas Campo Verde, Tutuaca, and Cascada de Basaseachi. Elevation ranges from 1,730 to 2,800 m. In the north of Sonora State occurring in Agua Prieta, Arizpe, Bacoachi, Bavispe, Cananea, Cucurpe, Huachinera, Fronteras, and Yécora municipalities. Common in Sierra de Los Ajos and Bavispe. Elevation ranges from 1,425 to 2,150 m. It grows on shallow and rocky soils, in canyon bottoms, on stream banks along canyons and ravines with steep slopes (40°–65°).

Associated taxa include *Abies concolor* Lindl. & Gordon, *Abies durangensis* Martínez, *Pinus chihuahuana* Engelm., *Pseudotsuga* sp. (Pinaceae), *Alnus oblongifolia* Torr. (Betulaceae), *Arbutus* sp. L. (Ericaceae), *Cupressus arizonica* Greene, *Juniperus deppeana* Steud. (Cupressaceae), *Junglans major* (Torr.) A.Heller (Juglandaceae), *Ostrya virginiana* K.Koch (Betulaceae), *Platanus wrightii* S.Watson (Platanaceae), *Prunus* sp., *Rubus arizonensis* Focke, (Rosaceae), *Quercus arizonica* Sarg., *Quercus rugosa* Née (Fagaceae), *Salix* sp. (Salicaceae), *Tilia* sp. (Malvaceae), *Toxicodendron radicans* Kuntze (Anacardiaceae), and *Yucca schottii* Engelm. (Asparagaceae).

Phenology. Flowers seen from March to May. Fruits present from May to September. Leaves turning scarlet and orange in October and new leaves observed in February and March.

Common Names. Palo azúcar (Sonora), guchachari (Tarahumara, Chihuahua).

Conservation Status. Species evaluted as of Least Concern (LC), under IUCN Red List guidelines (IUCN 2012).

TYPE: San Luis Mountains on the Mexican boundary line, 19 Jul 1892, *E.A. Mearns 535* (isotype: NY).

Specimens Examined. **MEXICO. Chihuahua.** San Luis Mountains, Devil's cañón, 1,889 m, 12 Aug 1908, *E.A. Goldman 1426* (US); **Casas Grandes municipality:** rio Gavilán, 11 km southwest of Pacheco, 1,800 m, 10 Aug 1948, *R.A. McCabe 62* (WIS); 113 km by road east of Vieja Casas Grandes, 29 Aug 1952, *J.M. Tucker 2570* (A, ARIZ); **Guachochic municipality:** Cusarare hot spring along arroyo Cusarare, 1,900 m, 17 Nov 1973, *R.A. Bye Jr. 5877* (GH, LL TEX, MEXU); barranca del Cobre, 7 May 1940, *I. Knobloch 7034* (US); **Madera municipality:** 11 km west of Chuhuichupa, 30 Sep 1939, *C.H. Muller 3575* (F, GH, LL TEX, MICH, MO, TENN); paraje de la Cueva Grande, 2,400 m, 4–8 Apr 1976, *J.C. Hernández s.n*. (MEXU); arroyo de la Quinta, antes del entronque los Marranos, 2,340 m, 24–25 Jun 1990, *O. Bravo 842, 843* (IEB, MEXU); cercanías de la Mesa del Huracán, 2,300 m, 10 Jun 1958, *E. Matuda 32684* (MEXU); rio Negro, camino a El Poleo, 1,920 m, 24 Jun 1990, *O. Bravo 827* (IEB, MEXU); **Ocampo municipality:** 10 km by road from San Juanito to Yécora, northwest of Basaseachic, 2,300 m, 10 Apr 1981, *F. Reichenbacher & L.J. Toolin 1339* (ARIZ); La Bateria, along rio la Haciendita, 1,600 m, 27 Jun 1986, *G. Ferguson & M. Rourke s.n*. (ARIZ); bottom of arroyo Durazno, ca 3 km upstream from La Bateria and 6 km by road from Pinos Altos, 1,730 m, 7 Jul 1994, *R.S. Felger 94-304* (ARIZ, LL TEX, MEXU, MO); arroyo La Cumbre just east of Ocampo, 24 Sep 1991, *G. Ferguson & B. Moon s.n*. (ARIZ); Basaseachic falls, 1,750 m, 26 Jun 1986, *G. Ferguson s.n*. (ARIZ), 12 Mar 1994, *A. García et al. 2568* (NY), 13 Oct 1980, *R.A. Bye 9853* (MEXU), 6 Jul 1936, *H. LeSueur 775* (F, GH, LL TEX), 19 Aug 1984, *G. Neson & P. Lewis 5098* (LL TEX); Virginia arroyo, Concheño, 1,981 m, 20 Jun 1946, *W.P. Hewitt 133* (GH); 2 km south of Cocheno, on road to highway 16 by Rio Delicias, 2,200 m, 28 Aug 1986, *P.S. Martin et al. s.n*. (ARIZ); rio Cocheno crossing highway 16, 1,550 m, 15 Aug 1987, *P.S. Martin et al. s.n*. (ARIZ); **Temósachi municipality:** Nabogame, 28 Aug 1987, *J.E. Laferrière 1000* (LL TEX), 21 Mar 1988, *J.E. Laferrière 2331* (ARIZ, MEXU), 6 Jul 1988, *J.E. Laferrière 1491* (ARIZ, MEXU); Highway 16 crossing of the rio Cocheno, 7 km northwest of Cocheno, 1,730 m, 3 Jul 1992, *P.S. Martin & D. Barber s.n*. (ARIZ, MEXU); **Sonora.** Huchuerachi, 4,000 m, 6 Dec 1890, *C.V. Hartman 308* (K); **Arizpe municipality:** Dead Bull Canyon, near Arizpe, 17 Mar 1982, *R. Thompson & O. Davis 82–34* (ARIZ); **Agua Prieta municipality:** Cañón Púlpito, 11 Oct 1939, *C. H. Muller 3720* (MICH, TENN); along stream in Cajón Bonito, 8 km upstream from Rancho Diablo and 5 km downstream from Rancho Nuevo, 1 May 1976, *C.T. Manson & R.E. McManus 3203* (ARIZ, MEXU); sierra San Luis, cajón Bonito at rancho Pan Duro, 24 Jul 1993, *R.S. Felger 93-505* (ARIZ, LL TEX, MEXU); **Bavispe municipality:** cañón de Bavispe, 25 Jul 1940, *S.S. White 3011* (GH, MEXU, MICH); cañón de El Temblor, 19 Aug 1940, *S.S. White 3390* (MEXU, MICH); el rancho del Roble, northeast of El Tigre, 1,828 m, 2–13 Sep 1941, *S.S. White 4318* (ARIZ, GH, LL TEX, MEXU, MICH); **Cananea municipality:** cañón Evans, 25 km east of Cananea and 12 km east of Ignacio Zaragosa, 1,660 m, 3 Jul 1983, *P.S. Martin s.n*. (ARIZ); Molino canyon, sierra de los Ajos, 1,645 m, 17 Jul 1952, *J.T. Marshall Jr. 68* (ARIZ); Casa de Piedra, cañón de Evans, 1,890 m, 9 Sep 1980, *J.S.C. & R.N.F. 131* (MEXU); Las Cabañas, rancho de los Ajos, cañón de Evans, 1,680 m, 8 Oct 1992, *R.S. Felger et al. 92-803*

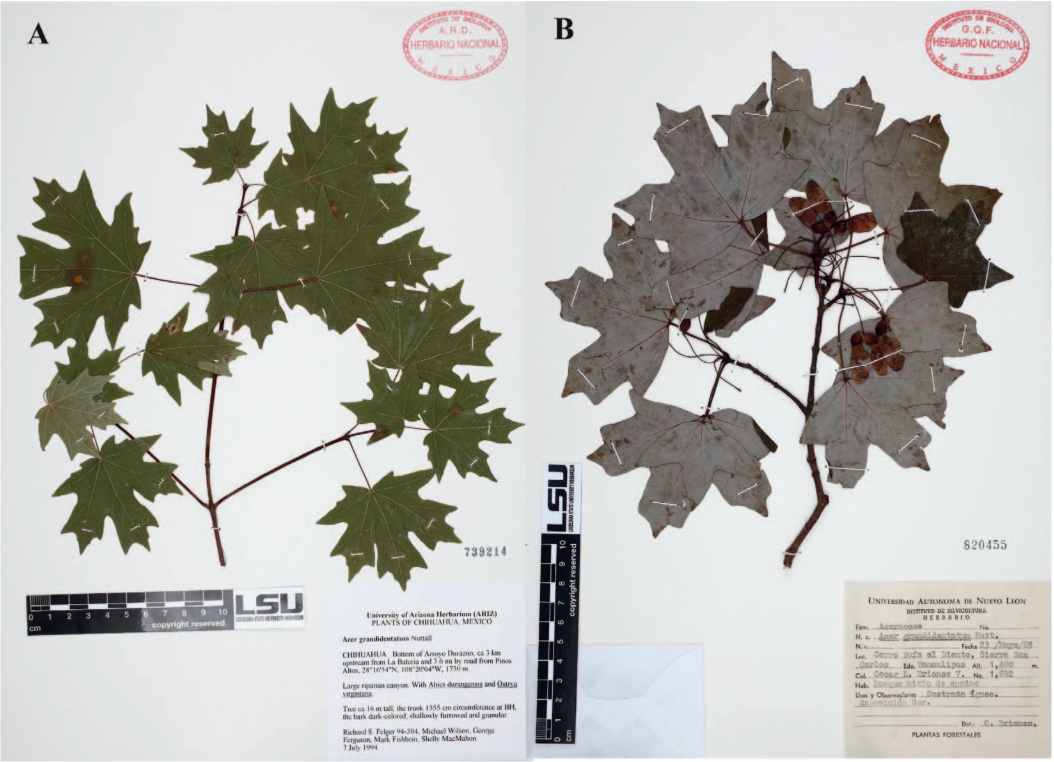

FIG. 8. Morphological variation of (A) *Acer grandidentatum* Nutt., leaves 4.2–11.1 × 3.7–13.9 cm; (B) *Acer grandidentatum* var. *sinuosum* (Rehder) Little, leaves 3.5–9.5 × 3.6–11.8 cm, few projections around the margin, rounded.

(ARIZ, MEXU); rancho de los Ajos, cañón de Evans, 1,650 m, 8 Oct 1992, *R.S. Felger et al. 92-791* (LL TEX, MEXU); **Cucurpe municipality:** La Brisca, 16 Nov 1982, *C. Drew & D.W. Steadman s.n*. (ARIZ); Puerto de los Aserraderos, 4–9 Aug 1940, *S.S. White 3205* (ARIZ, GH, MEXU, MICH); **Fronteras municipality:** arroyo Tierritas Blancas, 0.5 km east of Cerro Peñas Blancas, 2,080 m, 23 Apr 1995, *M. Fishbein 2323* (ARIZ, TEX LL, MEXU); sierra de los Ajos, cañón Frijolito, 2,300 m, 8 Oct 1992, *R.S. Felger et al. 92-860* (MEXU); arroyo Frijolito, 2,150 m, 9 Oct 1992, *M. Fishbein et al. 732* (ARIZ, LL TEX, MO); **Yecora municipality:** 3–4 km north-northwest of El Kipor (Quipur), 1,640 to 1,680 m, 4 May 1995, *T.R. Van Devender & A.L. Reina G. 95-394* (ARIZ, LL TEX); arroyo Hondo, 11.5 km east of El Kipor, 1,460 m, 13 March 1996, *T.R. Van Devender & S.L. Friedman 96-109* (ARIZ, LL TEX, MEXU), 28 May 1996, *A.L. Reina et al. 96-271* (ARIZ, MEXU), 28 May 1996, *V.W. Steinmann et al. 893* (ARIZ, BM, IBUG, IEB, MEXU, MICH, NY, XAL).

Acer grandidentatum var. ***sinuosum*** (Rehder) Little, Rhodora 46:449. 1944. *Acer grandidentatum* var. *brachypterum* Palmer, Jour. Arnold. Arb. 10:40. 1929. *Acer mexicanum* A. Gray, Proc. Am. Acad. 5:176. 1861. *Acer sinuosum* Rehder, Trees & Shrubs 2:255. 1913. *Acer saccharum* var. *sinuosum* (Rehder) Sarg., Bot. Gaz. 67:234. 1919. *Acer barbatum* var. *sinuosum* Ashe, Rhodora 24:79. 1922.

Tree 10–16 m tall, deciduous, stem 20–70 cm in diameter; bark dark grey, vertically furrowed. *Petioles* tomentose or glabrous. *Leaves* with 3–5 lobes, leaf base cordate or truncate (V-shape projection sometimes present in populations from Texas), minor lobes sometimes overlapping, lobe with a few projections around the margin, rounded; lamina 3.5–9.5 × 3.6–11.8 cm, midvein 2.8–9.3 cm, main lateral vein 2–8.2 cm, intersinus 1–3.1

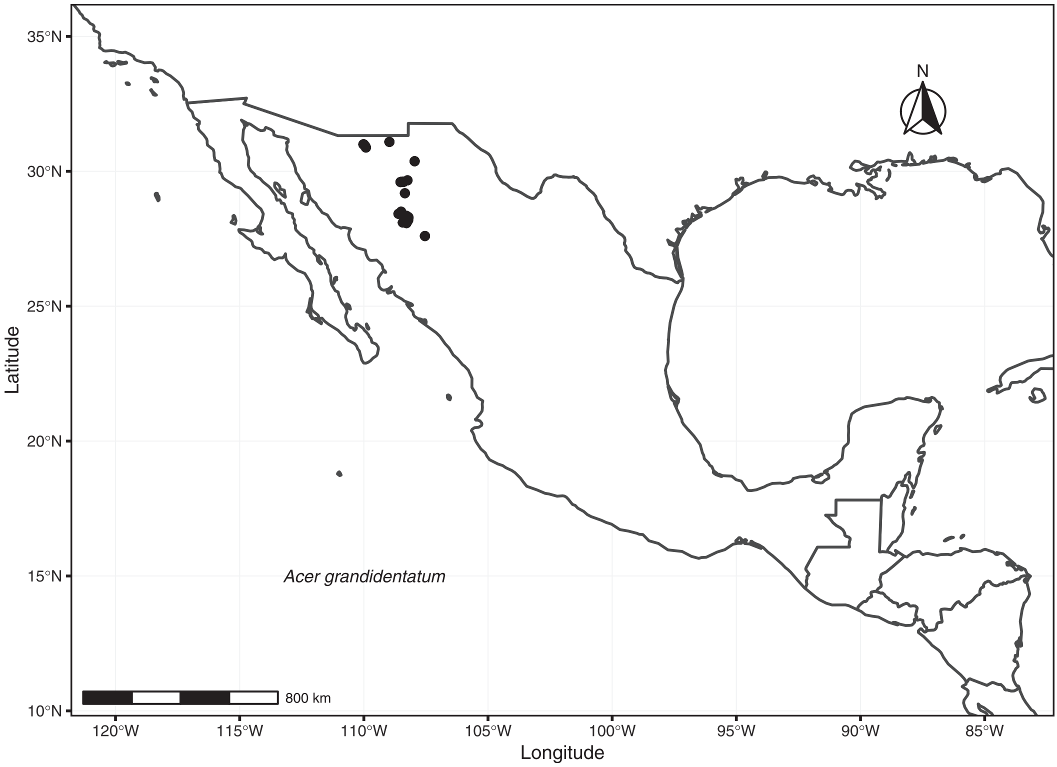

FIG. 9. Distribution of *Acer grandidentatum* Nutt. Black dots represent populations.

cm, horizontal vein 1.4–9.7 cm, abaxial side tomentose-villous. *Flowers* in corymbs, yellowish, apetalous, unisexual (plants with labile sex expression). *Perianth* connate, broadly campanulate, often with lobes, lanuginous along edge and at the base; perianth 1.4–3.8 × 1.9–4.2 mm. *Stamens* 6–8, filaments reddish, 2.5–4.6 mm long, the anthers 1.4–2.1 × 0.7–1.1 mm, oblong, attachment basifixed, distal connective protrusion absent. *Pistil* with style 0.5–2 mm, nectary disc 0.2–0.6 mm in height, stigma 1.3–5.4 mm sometimes persistent in the fruit. *Nutlet* elliptic, sparsely lanuginous, veins present, sometimes not inflated; 0.6–0.9 × 0.5–0.7 cm; distal keel absent or inconspicuous, nutlet contact scar 0.4–0.5 cm; *wings* with coalescent proximal veins sparsely distributed; wings 1.5–2.6 × 0.6–1.5 cm, wing sulcus 0.3–0.7 cm wide (Fig. 8b).

Distribution and Ecology. Northeastern Mexico: Coahuila, Nuevo León, and Tamaulipas states. Along Sierra Madre Oriental: northwestern and central Coahuila in the Castaños, Cuatro Ciénegas, Ocampo, Muzquiz, and Ramos Arizpe municipalities (Fig. 10). Some populations are inside the Maderas del Carmen protected natural area. Elevation range 1,100 to 2,250 m. In northwestern Nuevo León, occurring along the mountains in Bustamante and Lampazos de Naranjo municipalities and Sierra Gomas in Villaldana municipality. Elevation range 1,100 to 1,400 m. In western Tamaulipas a population is present in Cerro Bufa el Diente, San Carlos municipality. Elevation 1,400 m. Growing on gravelly and sandy loam derived from igneous rocks and calcareous soils on limestone. Ocurring in steep canyons and along streams. Associated taxa include *Cupressus arizonica, Juniperus ashei* J.Buchholz, *Juniperus flaccida* Schltdl. (Cupressaceae), *Fraxinus berlanderiana* DC., *Fraxinus cuspidate* Torr. (Oleaceae), *Garrya* sp. (Garryaceae), *Pinus arizonica* Engelm., *Pinus cembroides* Zucc., *Pinus ponderosa* P.Lawson & C.Lawson, *Pseudotsuga* sp. (Pinaceae), *Prunus serotina* Ehrh. (Rosaceae), *Quercus glaucoides* M.Martens & Galeotti, *Quercus grisea* Liebm., *Quercus gravesii* Sudw., *Quercus hypoleucoides* A.Camus, *Quercus mohriana* Buckley

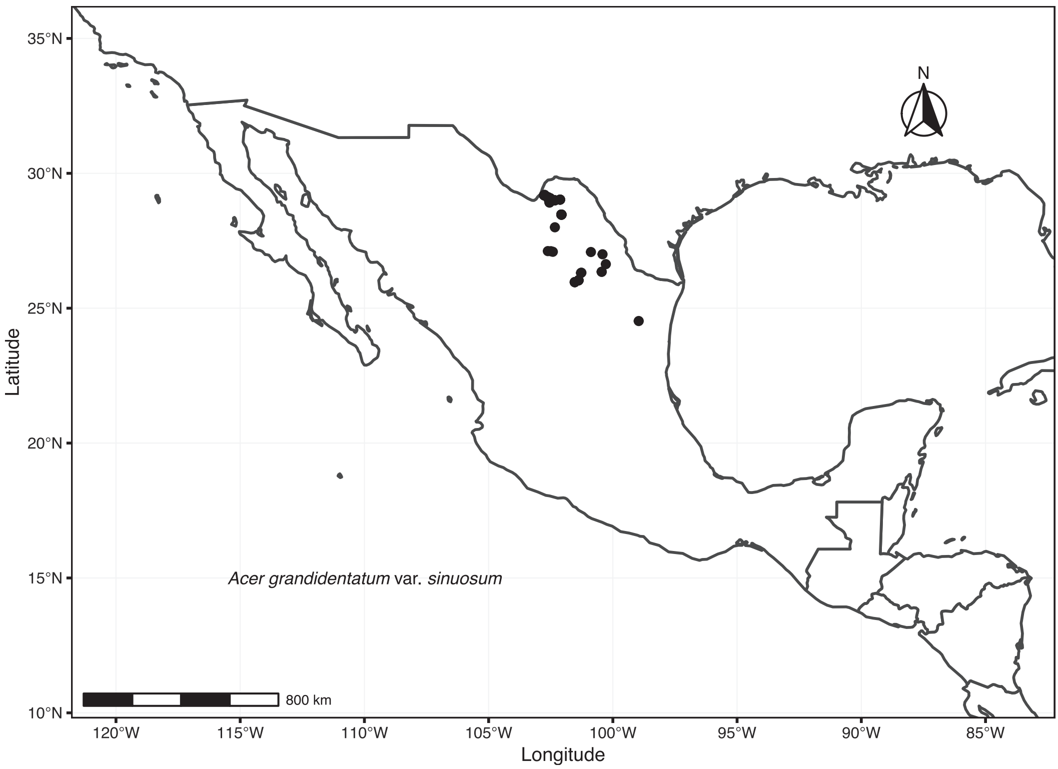

Fig. 10. Distribution of *Acer grandidentatum* var. *sinuosum* (Rehder) Little. Black dots represent populations.

(Fagaceae), *Salix* sp. (Salicaceae), *Styrax youngiae* Cory (Styracaceae), *Tilia* sp. (Malvaceae).

Phenology. Flowering from March to April and fruits observed from May to September.

Common Names. Palo de azúcar (Coahuila, Nuevo León).

Conservation Status. Species evaluted as Least Concern (LC), under IUCN Red List guidelines (IUCN 2012).

Specimens Examined. **MEXICO. Coahuila.** Mount Caracol, 21 m southeast of Monclova, Aug 1880, *E. Palmer s.n*. (GH); 5 km west of mouth of Canyon de la Hacienda, due west of El Coyote turnoff between Ocampo and Cuatro Ciénegas, 1,645 m, 10 Jul 1974, *R.G. Engard & M.L. Getz 303* (ARIZ, LL TEX); Sierra de la Madera, north side, lower part of Cañón de la Hacienda, 1,600 m, 11 May 1973, *M.C. Johnston et al. 10978* (LL TEX); **Acuña municipality:** Sierra Madera del Carmen, Rancho el Secadero, cañón Poblano, 20 Aug 1994, *M.A. Carranza et al. 2075* (IEB, LL TEX, MO), 28 Mar 19992, *M.A. Carranza et al. 1346* (ARIZ, IEB); Serranias del Burro, Rancho El Bonito, 3 May 1981, *D.H. Riskind et al. 2325* (LL TEX, MEXU), 11 Apr 1976, *D.H. Riskind et al. 1957* (LL TEX); cañón El Club at and above Rancho El Club in a tributary of cañón de Centinela, south of Pico de Centinela, 1,450 m, 31 Jul 1973, *M.C. Johnston et al. 11951* (F, LL TEX, MO, MEXU, NY); Sierra del Carmen in "Styrax canyon," 1,400 m, 6 Apr 1974, *T. Wendt 148A* (LL TEX, MEXU); Cañón del Diablo, Sierra del Carmen, 1,450 m, 10 Aug 1974, *T. Wendt 549* (LL TEX, MEXU); canyon Hundido on north side of Pico de Centinela, sierra del Jardin, 8 km east of Rancho El Jardin, 27 Jul 1973, *M.C. Johnston et al. 11798, 11808* (F, LL TEX, MO, NY); 17 km winding road north of El Jardin, ca. 5 km southwest of Mina El Popo, 28 Jul 1973, *M.C. Johnston et al. 11901* (LL TEX, MEXU); ca 32 km east-southeast of Boquillas in Sierra del Carmen, *ca*. 2.5 mi E of Rancho El Jardin, 1,645 m, 27 Jul 1973, *J. Henrickson 11400* (NY, US); **Castaños municipality:** *ca*. 5.6 km south of Monclova, 1,615 m, 3 Aug 1973, *J. Henrickson 11776* (LL

TEX); cañón de la Gavia above (south of) rancho de la Gavia, 1,000 m, 2–3 Aug 1973, *M.C. Johnston et al. 12035K* (LL TEX); **Cuatro Ciénegas municipality:** Sierra de la Madera, Cañón del Pajarito, 6 Sep 1939, *C.H. Muller 3189* (GH, LL TEX, MICH, NY); Cañón los Olmos, 1,975 m, 17 Aug 1975, *T. Wendt & E. Lott 1191* (LL TEX); **Candela municipality:** Sierra Pájaros Azulez, Campo Santa María, 24 Jun 1997, *P. Cruz 48* (IEB); **Monclova municipality:** Gloria Mountains, 31 Jul 1939, *E.G. Marsh Jr. 1868* (F); Monclova, Jul 1939, *E.G. Marsh 1868* (LL TEX); **Múzquiz municipality:** Rincón de María, 1,100 m, 18 Sep 1999, *J.A. Villarreal et al. 8738* (LL TEX, NY, MEXU, MO, US); Cañón de Milagro, eastern side of the Sierra de los Guajes, about 12 km west of Hacienda de la Encantada, 10–16 Sep 1941, *R.M. Stewart 1529* (F, GH, LL TEX); *ca*. 86.9 km northwest of Múzquiz, in the Rincón de María region of the limestone Sierra de la Encantada (Sa. de Santa Rosa), 1,100 m, 18 Sep 1999, *J. Henrickson 22567* (IEB, LL TEX, MEXU); Rincón de María, on Hacienda La Babia, *ca*. 112 km by road northwest of Múzquiz, 27 Apr 1975, *T. Wendt & D. Riskind 920* (LL TEX, MEXU); Sierra la Babia, Rincón de María en el rancho la Babia, 1,040 m, 16 Sep 1999, *J.A. Villarreal et al. 8802* (IEB, MEXU); Rancho Agua Dulce, 30 Jun 1936, *F.L. Wynd & C.H. Mueller 389* (A, ARIZ, NY, MO, US); **Ocampo municipality:** Sierra Maderas del Carmen, cañón El Dos, *ca*. 1.2 km up (west) from Campo Uno, and below junction with C. El Oso, 1,850 m, 3 Apr 1974, *T. Wendt et al. 127A* (LL TEX); north of Picacho del Centinela, del CarmenMountains, 24 Aug 1953, *B.W. Warmock 11579* (LL TEX); *ca*. 40 km southeast of Boquillas, in Sierra del Carmen, canyon El Club near Rancho El Club, 1,737 m, 31 Jul 1973, *J. Henrickson 11622* (LL TEX, WIS); *ca*. 86.9 km southeast of Big Bend National Park, cañon de la Fronteriza, 1.6–5 km northwest of Rancho San Isidro, at end of Canyon del Alamo, 6 Aug 1976, *J. Henrickson 15007* (MEXU, NY); **Ramos Arizpe municipality:** El Cedral, Sierra de Paila, 1300 to 1600 m, 16 Oct 1986, *J.A. Villarreal et al. 3550* (ARIZ, MEXU), 4 Oct 1989, *J.A. Villarreal et al. 5262* (IBUG, LL TEX, MEXU, XAL), 12 May 1989, *A. Rodriguez 1092* (ARIZ, NY, MEXU), 23 Mar 1990, *A. Rodriguez et al. 1328* (MO); **Nuevo León. Bustamante municipality:** Rancho Minas Viejas, 1,400 m, 2 May 2001, *J.A. Villarreal et al. 9108* (LL TEX); **Lampazos de Naranjo municipality:** arroyo el Campanero, 3 km al SO del casco del rancho Rezendiz, 500 m, 13 Jul 1985, *O. Briones 1871* (MEXU); rancho Resendez, 24 Jun 1937, *M.T. Edwards 362* (F, LL TEX, MEXU, MO, NY); **Villaldama municipality:** sierra Gomas, in canyon El Alamo, 15 Aug 1988, *T.F. Patterson 6684, 6685* (LL TEX); **Tamaulipas. San Carlos municipality:** Bufa el Diente, sierra San Carlos, 1,400 m, 11 Oct 1984, *O. Briones 1191* (IBUG, MEXU, MO), 21 Mar 1985, *O. Briones 1476, 1477* (MEXU, MO), 23 May 1985, *O. Briones 1692* (MEXU), 17 Jun 1987, *G. Nesom 6117* (LL TEX, NY); originally growing in sierra San Carlos and planted in Peckerwood Garden, 10 Nov 2016, *Y.L. Vargas-Rodriguez 1852* (LSU).

Discussion About the *A. grandidentatum* Group. *Acer grandidentatum* has been subordinated as a subspecies of *A. saccharum* (*A. saccharum* subsp. *grandidentatum* and *A. saccharum* var. *sinuosum*) by Sargent (1919), Desmarais (1952) and most recently by van Gelderen *et al*. (1994). Van Gelderen *et al*. (1994) did not consider inflorescence and flower characters for the species classification and accepted the view of Desmarais (1952), although they acknowledged that it could be a species on its own. The present work uses leaf, flower, and fruit morphologies to support its species status. The taxon has been previously treated as species in different regional flora treatments (Wooton and Standley 1915, Correll and Johnston 1970, Welsh *et al*. 1987, Cronquist *et al*. 1997, Diggs *et al*. 1999). Thus, two entities of *A. grandidentatum* are identified: *A. grandidentatum* from western USA to western Mexico and *A. grandidentatum* var. *sinuosum* present in the eastern side of the White Sands National Monument (eastern New Mexico) and throughout Texas and eastern Mexico.

Previous studies found morphological differences to separate two different taxa. Murray (1980b) indicates two varieties of *grandidentatum*: one corresponds to northwestern Mexico (Chihuahua and Sonora) and other to northeastern Mexico (Coahuila). Van Gelderen *et al*. (1994) corroborate that the variety *sinuosum* is distributed in Texas without mentioning its presence in Mexico, and that the variety *grandidentatum* is confined to western North America.

Acer grandidentatum var. *sinuosum* is distributed in eastern Mexico and has populations in eastern New Mexico and Texas. Some populations from Texas resemble the eastern USA species *A. saccharum* subsp. *floridanum* and could potentially form hybrids with it. *Acer grandidentatum* var. *sinuosum* is distinguished by the morphology of the main central lobe of the leaf, which has parallel to slightly divergent sides in *A. saccharum* subsp. *floridanum*, but strongly divergent sides in *A. grandidentatum*. In addition, the central lobe often tapers from the base in *A. saccharum* subsp. *floridanum*, whereas the leaf texture is thicker in *A. grandidentatum*. *Acer grandidentatum* var. *sinuosum* resembles *A. grandidentatum* in having the leaves with broader sinuses and lobes with a few tooth projections and the flowers with a lobed calix, but differs from the same by having the leaves broader than long and fewer and shorter tooth projections and the flowers with larger styles but shorter stigmas.

The populations of *A. grandidentatum* that occur in Arizona, Chihuahua, Colorado, New Mexico, Sonora, and Utah are geographically isolated from *A. saccharum* subsp. *floridanum*, forming a well-differentiated group that cannot be confused with *A. saccharum* subsp. *floridanum*. The type material of *Acer brachypterum* and *A. saccharum* subsp. *brachypterum* collected in San Luis Mountains (E. A. Mearns 535) corresponds to *A. grandidentatum*.

Acer skutchii Rehder, J. Arnold Arbor. 17: 350. 1936. *Acer saccharum* subsp. *skutchii* (Rehder) Murray Kalmia 7:18. 1975.

Tree 20–30 m tall, deciduous, stem 60–75 cm in diameter, bark smooth, gray to whitish or auburn-reddish, with scaly thin plates that peel in old trees. *Petioles* tomentose or sparsely villous; buds ovate 3–4 × 2–3 cm, scale pairs 3–5, appressed silky white hair along scale edge, basal scale with prickle 0.1–0.7 mm. *Leaves* with 3, 4, or 5 lobes, leaf base cordate, minor lobes sometimes present, occasionally overlapping, teeth projections around the margin 1–22, acute or lobed; lamina 6.4–19.2 × 5.9–23.8 cm, radius 3.9–10 cm, midvein 6–17.4 cm, main lateral vein 4.8–18.7 cm, intersinus 2.1–8.2 cm, horizontal vein 1.6–8.8 cm, abaxial side lanuginous, scarcely villous along the edges, abaxial trichomes with long nodulations. *Flowers* in corymbs, apetalous sepals present, unisexual (plants monoecious). *Perianth* connate, sparsely villous along the edge and the base; perianth 1.9–3.5 × 1.3–2.9 mm. *Stamens* 4–8, filaments 1.4–4.6 mm long, the anthers 1.5–1.8 × 0.5–0.7 mm, oblong, base cordate, trichomes absent, distal connective protrusion absent. *Pistil* with style 0.7–2 mm, nectary disc 0.2–0.5 mm, stigma 2.3–5.8 mm; male flowers with abortive pistil villose and stigma 0.2–0.5 mm. *Nutlet* square-like (sometimes rounded in some trees from Tamaulipas), glabrous or sparsely villous, smooth surface sometimes veined, extremely inflated; 0.4–1.1 × 0.6–1.1 cm, distal keel present often inconspicuous, proximal keel sometimes protruding, nutlet contact scar 0.4–0.75 cm; seed spheroid 0.3–0.5 cm; *wings* proximal side straight, sometimes slightly curved, wing divergence angle 6°–51°, venation with abundant anastomoses and bifurcating towards distal part, reticulate veinlets abundant; wings 1.8–4 × 0.4–1.6 cm, wing sulcus 0.3–0.6 cm wide (Fig. 11a,c).

Distribution and Ecology. Northeastern and southern Mexico (Tamaulipas and Chiapas states) and central Guatemala. Present in Tamaulipas at El Cielo Biosphere Reserve. In southern Mexico in Tenejapa municipality, Chiapas State. In Guatemala, it is found in the Sierra de las Minas Biosphere Reserve (El Progreso and Zacapa Departments) and Nebaj, Quiche Department (Fig. 12). It occurs at 1,481 m elevation in northern Mexico and higher elevations in southern Mexico and Guatemala (1,750–2,210 m). The areas are characterized by mean annual temperature of 13°–16°C and mean annual precipitation of 917–1,011 mm. It grows on limestones and Leptosol soils. In Guatemala, the species grows along ravines and streams in cloud forests on Sierra de las Minas and Quiche. In the south of Mexico it is distributed in a remnant cloud forest in Chiapas, surrounded by pasturelands, and in the north of Mexico in a cloud forest of the El Cielo Biosphere Reserve. Associated taxa include *Liquidambar styraciflua* (Altingiaceae), *Carpinus caroliniana* Walter (Betulaceae), *Cornus disciflora* (Cornaceae), *Pinus* spp. (Pinaceae), and *Quercus* spp. (Fagaceae) (Vargas-Rodriguez and Platt 2012). Tree density is estimated at 234/ha in Tamaulipas, 32/ha in Chiapas, and 85/ha in Guatemala (Vargas-Rodriguez and Platt 2012). The populations have increased homozygosity and low genetic diversity, indicating bottlenecks lasting many generations (Vargas-Rodriguez *et al*. 2015).

Phenology. Leaves appearing from January to early February, turning red in November and

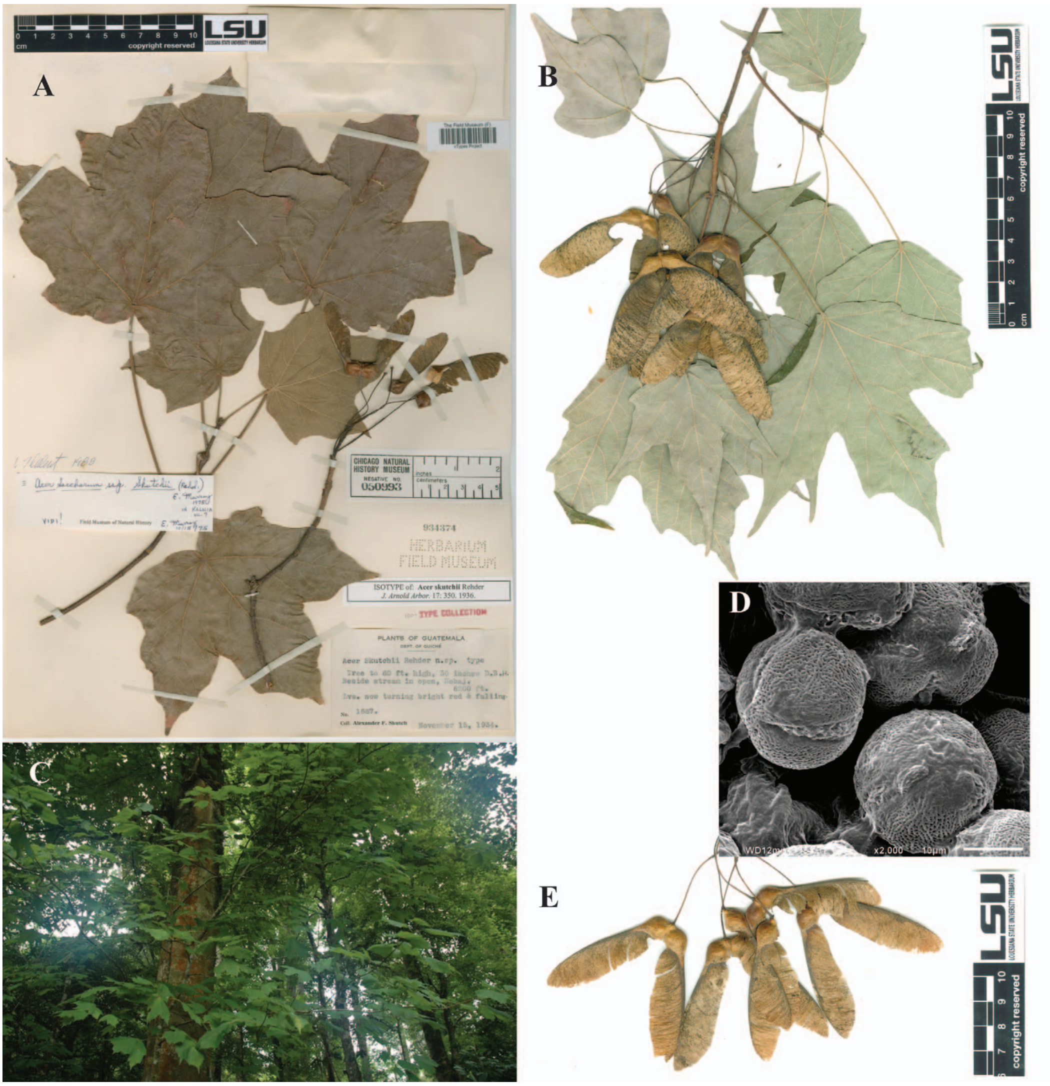

FIG. 11. Type of (A) *Acer skutchii* Rehder and (B) *Acer binzayedii* Vargas-Rodriguez. (C) A standing tree of *A. skutchii* in Sierra de las Minas Biosphere Reserve, Guatemala. (D) Suboblate spheroid pollen grain of *A. binzayedii* with exine striate-reticulate. (E) Unattached fruits of *A. binzayedii* from Y.L. Vargas-Rodriguez 389 (LSU).

falling in December. Mature fruits from July to August.

Common Names. Álamo plateado, haya, maple.

Conservation. Species evaluted as Critically Endangered CR B2ab(iii,v), under IUCN Red List guidelines (IUCN 2012, Vargas-Rodriguez *et al.* 2017a). Two populations were included in the biosphere reserves: Sierra de las Minas (Guatemala) and El Cielo (Mexico). Forest fires, coffee plantations, corn fields, and mining are present in the surrounding areas, and conversion of land to coffee plantations is accelerated in Guatemala.

TYPE: GUATEMALA. El Quiché: Nebaj Departamento, 1,889 m, 15 Nov 1934, *A.F. Skutch 1667* (isotype: BM, F, NY).

Specimens Examined. **GUATEMALA. Guatemala:** jardines de la Universidad del Valle, 27 Apr 2003, *Y.L. Vargas-Rodriguez & E. Medinilla 348* (LSU), 28 Apr 2003, *Y.L. Vargas-Rodriguez 267* (BIGU), 14 Nov 1995, *E. Pöll 5302* (UVAL), 28 Apr 2003, *E. Pöll s.n*. (UVAL); 4 Jun 2010, *Y.L.*

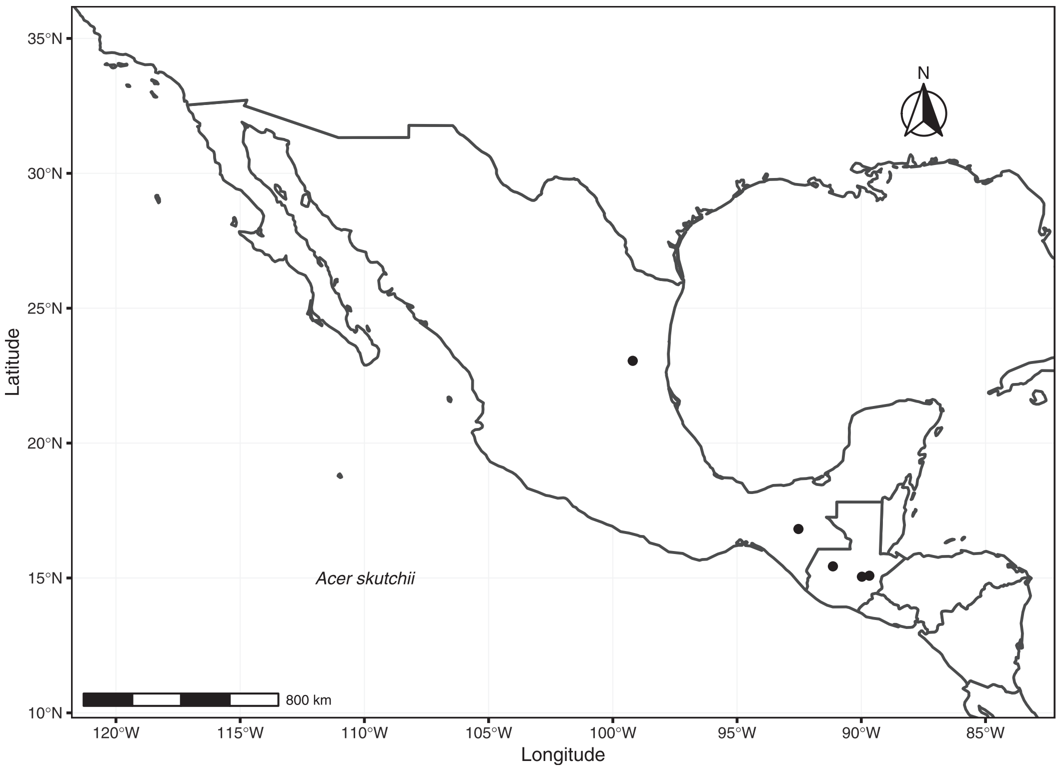

Fig. 12. Distribution of *Acer skutchii* Rehder. Black dots represent populations.

Vargas-Rodriguez & C.I. García-Jiménez 1488–1494 (LSU); **El Progreso:** El Balsamal, 23 Apr 2003, *Y.L. Vargas-Rodriguez & I. Nájera 346* (LSU), 22 May 2010, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1334, 1336–1340, 1342–1401* (LSU); Aldea Los Albores, 26 Apr 2003, *Y.L. Vargas-Rodriguez & I. Nájera 347* (LSU); Finca La Tormenta, 22 May 2010, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1402–1423* (LSU); **El Quiché:** Nebaj, 28 May 2010, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1459–1486* (LSU); along river below Nebaj, 1,828 m, 5 Feb 1945, *A.J. Sharp 4567* (F, GH, TENN), 6 Feb 1945, *A.J. Sharp 4588* (F, GH, MEXU, NY, TENN), 8 Feb 1946, *A.J. Sharp 4692, 4693* (F, GH, MEXU, MO, NY, TENN); north of Nebaj, 1,767 to 1,828 m, 25 Jun–17 Aug 1964, *G.R. Proctor 25206* (F, LL TEX, MO); **Zacapa:** along rio Repollal to summit of mountain, 2,100 to 2,400 m, 12–13 Jan 1942, *J.A. Steyermark 42537* (A, EAP, F, MICH, NY, US); Zacapa, 15 Apr 2007, *E.A. Gil 1* (AGUAT); San Lorenzo, 1,600 m, 24 Jan 1942, *J.A. Steyermark 43164, 43185* (A, F), 1,776 m, 25 May 2010, *Y.L. Vargas-Rodriguez & C.I. García-Jiménez 1424–1447* (LSU); quebrada Ojo de Agua, a tributary to Rillito de Monos, 16 Jan 1942, *J.A. Steyermark 42756* (A, F, NY);

MEXICO. Chiapas. Tenejapa municipality: camino a El Retiro, 18 Apr 2003, *Y.L. Vargas-Rodriguez 251, 253* (LSU), 9 Aug 2008, *Y.L. Vargas-Rodriguez 696* (LSU); Cañada Grande, 21 Apr 2003, *Y.L. Vargas-Rodriguez 302, 303* (LSU), 8 Aug 2008, *Y.L. Vargas-Rodriguez 689–695* (LSU); Refugio, 9 Aug 2008, *Y.L. Vargas-Rodriguez 697–796* (LSU); milpa El Mosco, 14 Sep 1953, *F. Miranda 7896* (MEXU); **Tamaulipas. Gómez Farías municipality:** 1 km antes de Rancho El Cielo, 3 Sep 2003, *Y.L. Vargas-Rodriguez 417* (LSU); arriba de La Colmena, 31 Aug 2003, *Y.L. Vargas-Rodriguez 390* (LSU); Agua del Indio, 27 Jun 2008, *Y.L. Vargas-Rodriguez 569–578* (LSU); Agua Escondida, 28 Jun 2008, *Y.L. Vargas-Rodriguez 599–608* (LSU); Casa de Piedra, 28 Jun 2008, *Y.L. Vargas-Rodriguez 629–638* (LSU), 24 Aug 1981, *H. Puig 7217* (IEB), 3 Jun 1953, *P.S. Martin 34* (MICH); La Colmena, 28 Jun 2008, *Y.L. Vargas-Rodriguez 659–688* (LSU), 24 Jul 1981, *H. Puig 7039*

(MEXU); company road to La Joya de Salas, at Rancho El Cielo, 24 Aug 1950, *A.J. Sharp & E. Hernández X. 50161* (TENN); near Rancho El Cielo, above Gómez Farías, 27–29 Aug 1950, *A.J. Sharp & E. Hernández X. 50283* (GH, MEXU, NY, TENN), 28 Aug 1950, *A.J. Sharp et al. 52207* (TENN), 28 Aug 1952, *A.J. Sharp et al. 52171, 52173* (TENN), 1 May 1967, *A. Gómez-Pompa 2012* (GH, MEXU, MICH); Rancho El Cielo, above Gómez Farías, 23 Aug 1950, *A.J. Sharp & E. Hernández X. 5066* (TENN); from El Cielo to Ojo de los Indios, 27 Aug 1952, *A.J. Sharp et al. 52115* (TENN), 25 Aug 1950, *50231* (GH, MEXU, TENN); cañón de Tableta, 2 Sep 1952, *A.J. Sharp et al. 52284* (TENN); vicinity of Gomez Farías, 1,097 m, 10 Jun 1949, *B.E. Harrell 189* (TENN); Rancho El Cielo, 19–22 Apr 1990, *S. Zamudio & A. Contreras 7835* (IEB, MEXU, XAL), 1,260 m, 15 Apr 1984, *S. Avendaño & H. Narave 1673* (IBUG, IEB), 11 Aug 1991, *H.H. Iltis & B. Simon 30632A, 30652A* (WIS), 22 Sep 1974, *F. González 7422* (MEXU), 10 Jun 1971, *J.R. Sullivan 420* (LL TEX, NY); Indian Springs 5 km southwest of Rancho El Cielo, 1,371 m, 29 Jul 1965, *L.E. Gilbert 57, 58* (LL TEX); Malecate, 29 Aug 1968, *A. Richardson 846* (LL TEX); El Paraiso a 7 km al W de Rancho El Cielo, 25 Sep 1974, *F. González 7491* (MEXU).

Acer binzayedii Vargas-Rodriguez, Brittonia 69:247. 2017.

Tree 20–30 m tall, deciduous, stem 60–90 cm in diameter; bark grey with long vertical ridges. *Petioles* tomentose to sparsely villose or glabrous, auburn; buds conical, 2–3.5 × 1–2 mm, scale pairs 3 or 4, basal scale prickle is inconspicuous or absent. *Leaves* with 5 lobes, leaf base cordate, minor lobes sometimes present, teeth projections around the margin 6–14, acute or lobed; lamina 6.4–19.2 × 6.1–19.4 cm, radius 3.9–10.3 cm, midvein 5.8–17.2 cm, main lateral vein 5.2–16.5 cm, intersinus 2.6–6.9 cm, horizontal vein 2.4–9.1 cm, abaxial side villous-tomentose, abaxial trichomes with short nodulations of reduced prominence. *Flowers* in corymbs, light yellow, apetalous, sepals present, unisexual (plants monoecious). *Perianth* connate, sparsely villous along the edge and at the base; perianth 2.7–3.5 × 2.5–3.6 mm. *Stamens* 6–9, filaments 3.5–5.8 mm long, the anthers 1.7–2.6 × 0.8–1.2 mm, oblong, base deeply sagittate, attachment subbasifixed, with scattered trichomes, papillate, distal connective protrusion sometimes present with mucronate shape; pollen tricolpate, suboblate spheroid, 3 furrows, exine striate-reticulate, with coarse reticulum, polar axis 20.8–39.4 μm, equatorial diameter 23–30.5 μm. *Pistil* with style 0.5 mm, nectary disc 0.3–0.5 mm in height, stigma 3–4 mm; male flowers with abortive pistil densely villose and stigma 0.6–0.9 mm. *Nutlet* elliptic, sparsely villous, hair yellowish, veins present, sometimes rugose, extremely inflated; 0.8–1.1 × 0.8–1.1 cm; distal keel present, proximal keel protruding, nutlet contact scar 0.7–1 cm; *seed* spheroid 0.5–0.7 cm; *wings* elliptic, wing divergence angle 17°–63°; coalescent proximal veins and anastomoses sparsely distributed, reticulate veinlets sometimes present; wings 3.5–5.6 × 1.3–2.5 cm, wing sulcus 0.6–1.1 cm wide (Fig. 11b,d,e).

Distribution and Ecology. Western Mexico, Jalisco State: Cañada de la Moza (Sierra de Manantlán), Ojo de Agua del Cuervo (Sierra de Cacoma); and Guerrero State (Fig. 13). Present from 1,790 to 1,880 m elevation, in areas with mean annual temperature of 18.5 °C, mean annual precipitation of 1,257 to 1,294 mm. Substrates in the area are intermediate extrusive rocks and Cambisol soils. The species is found in remnant cloud forests in ravines. Patches are surrounded by *Pinus-Quercus* forests. Co-occurs with *Carpinus caroliniana, Ostrya virginiana* (Betulaceae), *Cornus disciflora* (Cornaceae), *Dendropanax arboreus* (L.) Decne. & Planch. (Araliaceae), *Quercus salicifolia* Née (Fagaceae), and others (Vargas-Rodriguez and Platt 2012). Basal area and density of maples $\geq$ 1 cm diameter at breast height in the two populations was estimated to 18 m²/ha and 327 tree/ha, respectively (Vargas-Rodriguez and Platt 2012).

Phenology. Leaves appear in January and turn red in October. Flowering from December to January. Fruits forming in March and reaching maturity in August.

Common Names. Algodoncillo.

Conservation Status. Species evaluted as Critically Endangered CR B1ab(i,ii,iii,v)+2ab(i,ii,iii,v) under IUCN Red List guidelines (IUCN 2012, Vargas-Rodriguez 2017). One population is inside of a biosphere reserve. Abundance of the seedlings and saplings is low. Logging, forest fires, and sporadic cattle grazing are common in areas surrounding the *Acer* populations (Vargas-Rodri-

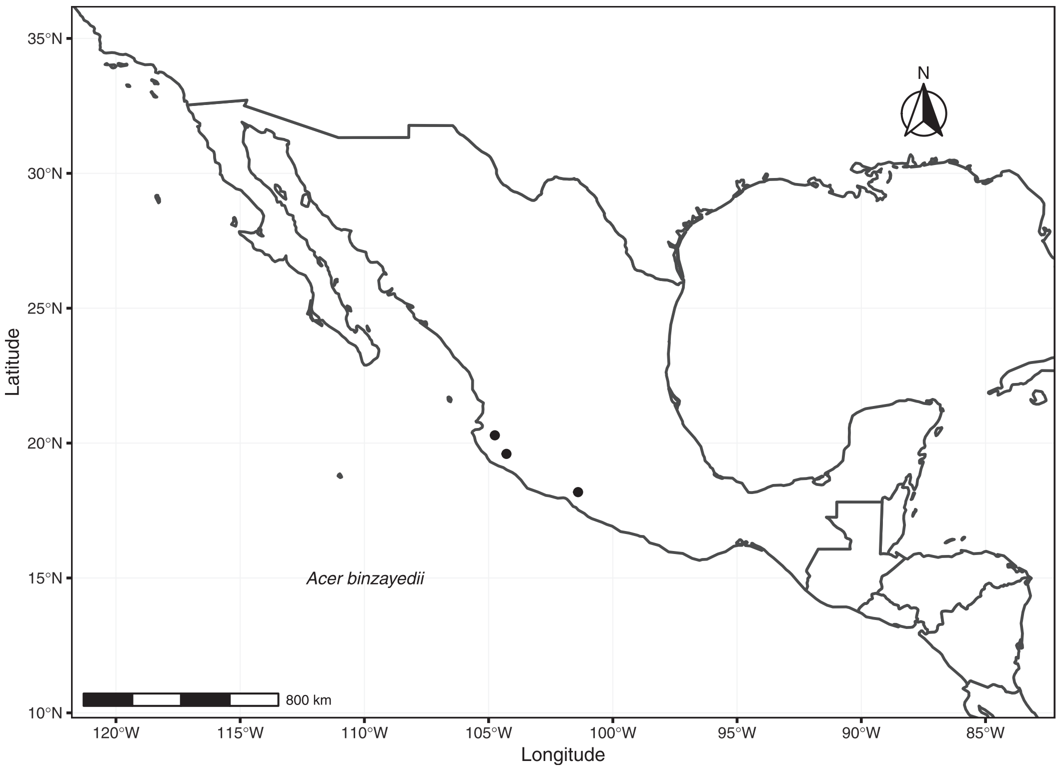

FIG. 13. Distribution of *Acer binzayedii* Vargas-Rodriguez. Black dots represent populations.

guez and Platt 2012, Vargas-Rodriguez *et al.* 2017b).

TYPE: MEXICO. Jalisco: Autlán de Navarro municipality: cloud forest, Cañada La Moza, 1,850 m, 19 June 2003, *Y.L. Vargas-Rodriguez & F. Vargas-Aguilar 373* (holotype: LSU; isotypes: GH, MO, NY, US, ZEA)

Specimens Examined. **MEXICO. Guerrero. Coahuayutla de José María Izazaga municipality:** Primer Campo, 1.36 km al SE, 25 Apr 2000, *R. Mayorga 1519* (IEB); Primer Campo, 8–11 Oct 2006, *Y.L. Vargas-Rodriguez et al. 525–558* (LSU); **Jalisco. Autlán de Navarro municipality:** Arroyo La Moza, ejido de Ahuacapán, 1,850 m, *A. Santiago 4* (WIS); 3.5 km al NW de la ECLJ, Cañada La Moza, 1850 m, 30 Mar 1991, *E. Jardel et al. 195, 196* (WIS, ZEA), 4 Apr 1991, *E. Jardel et al. 321, 322* (WIS, ZEA), 4 Aug 1991, *E. Jardel et al. 323* (WIS, ZEA), 4 Nov 1991, *E. Jardel 324* (MICH, WIS, ZEA); cañada La Moza, 2.5 km al NE de El Zarzamoro, 1,800 m, 8 Jun 1991, *R. Cuevas & E. Jardel 4157, 4158* (ZEA); 1.3 km by road due southeast of Corralitos toward Las Joyas, 1,840 m, 19 Jun 1991, *T. Cochrane & A. Vázquez 12612* (IBUG, F, MICH, WIS, ZEA,); cañada de La Moza, 3.5 km al NE de Las Joyas, 1,850 m, 4 Apr 1992, *E. Jardel & A. Santiago 325-330* (IEB, MICH, WIS, ZEA); La Moza, just downslope from road west of Las Joyas on road to Ahuacapán, *ca*. 2 km southeast of Corralitos (Ejido Ahuacapán), 1,880 m, 8 Mar 1992, *H. Iltis et al. 30960* (MICH, WIS, ZEA); cañada La Moza, Estación Científica Las Joyas, 7 Sep 1994, *R. Cuevas & L. Guzmán 4620* (ZEA); cañada La Moza, 1,850 m, 19–20 Jun 2003, *Y.L. Vargas-Rodriguez & F. Vargas-Aguilar 371, 372* (LSU, ZEA), 20 Aug 2008, *Y.L. Vargas-Rodriguez & F. Vargas-Aguilar 851–875* (LSU); **Talpa de Allende municipality:** Ojo de Agua del Cuervo, 1,798 m, 12 Jul 2003, *Y.L. Vargas-Rodriguez 389* (LSU), 24 Jun 2005, *Y.L. Vargas-Rodriguez 798–809* (LSU), 5 Feb 2006, *Y.L. Vargas-Rodriguez 1716–1717* (LSU), 19 Aug 2008, *Y.L. Vargas-Rodriguez 810–850* (LSU), Mar 2015, *Y.L. Vargas-Rodriguez et al. 1802* (LSU).

DISCUSSION ABOUT *A. SKUTCHII* AND *A. BINZAYEDII*. *Acer skutchii* was subordinated to a subspecies of *A. saccharum* in the treatment by van Gelderen *et* *al*. (1994). Upon the examination of the anther ornamentation, perianth and anther length, fruit size and shape, length of wing and its sulcus, and leaf trichome ornamentation, *A. saccharum* subsp. *skutchii* was elevated to the species status (Vargas-Rodriguez *et al*. 2017b). In addition, *A. binzayedii*, previously considered within the same subspecies (*A. saccharum* subsp. *skutchii*), was differentiated and proposed as a new taxon (Vargas-Rodriguez *et al*. 2017b).

Acer skutchii and *A. binzayedii* are distinguished by the fruit, flower, and leaf characters and their geographic distribution. In *A. skutchii,* the perianth and stamen filaments are smaller, the anthers have cordate base lacking distal protrusion, and fruits are smaller, with a very narrow wing sulcus. In contrast, *A. binzayedii* has larger perianth and stamen filaments, the anthers are subbasifixed and mucronate with a deeply sagittate base, sometimes with a distal connective protrusion, and fruits are larger and with wider wing sulcus (Vargas-Rodriguez *et al*. 2017b). Some adult individuals of *A. skutchii* from the population in Tamaulipas have smaller and rounded fruits, while other characters remain consistent with the variations observed in the rest of the populations. *Acer skutchii* typically grows in limestones soils and it is tolerant to alkalinity, while *A. binzayedii* occurs in Cambisol soils and extrusive rocks (Vargas-Rodriguez and Platt 2012, Vargas-Rodriguez *et al*. 2017b). *Acer skutchii* is restricted to Tamaulipas, Chiapas (Mexico), and Guatemala, while *A. binzayedii* grows in western Mexico, in the states of Jalisco and Guerrero. Temperate genera with disjunct distribution growing in the same cloud forests containing *A. skutchii* and *A. binzayedii* comprise 20% of the total composition (*e.g*., *Carpinus* L., *Liquidambar* L., and *Cornus* L.) (Vargas-Rodriguez and Platt 2012). The disjunct distribution of some of those temperate hardwood species in cloud forests in Mexico and Central America could be the result of glacial and interglacial periods shifting the range of the populations (Graham 1999).

Acer skutchii and *A. binzayedii* differ from the geographically close species *A. saccharum* subsp. *floridanum* in wider but shorter perianth and the presence of a prominent distal connective protrusion of the anther. *Acer saccharum* is distinguished from *Acer skutchii* and *A. binzayedii* in recessed or elongated nodulations of the abaxial leaf trichomes, anther with a distal mucronate-type connective protrusion, and the smaller size of the nutlet (0.6 × 0.8 cm). *Acer skutchii* has populations in eastern and southern Mexico and Guatemala, and thus, it is the species with southernmost distribution in the *Saccharodendron* series (sugar maples) (Vargas-Rodriguez and Platt 2012).

PHYLOGENETIC RELATIONSHIPS OF MEXICAN AND CENTRAL AMERICAN *ACER* SPECIES. The length of the ITS region within the North American species analyzed here ranged from 649 to 651 bp. The ITS-1 region was 219–238 bp long, the length of the 5.8S subunit was constant at 163 bp, and the length of ITS-2 varied from 224 to 260 bp. The aligned matrix of the entire ITS region (ITS-1, 5.8S subunit, and ITS-2) was 763 bp long. From the total number of characters, 369 (48%) characters were constant, 165 (21.4%) variable characters were parsimony uninformative, and 234 (30.4%) characters were parsimony informative. The uncorrected pairwise distance between taxa ranged from 0% to 4.5% between the *A. negundo* samples from the USA and the Mexican and Central American samples. The uncorrected pairwise distance between *A. grandidentatum* and *A. grandidentatum* var. *sinuosum* was 2.3%. The length of the chloroplast intergenic spacers *ndhF–rpl32R* and *psbJ–petA* was 925 bp and 899 bp, respectively, while the concatenated matrix was 1,824 bp. The *ndhF–rpl32R* spacer contained an 11-bp insertion in all samples of *A. grandidentatum*, *A. grandidentatum* var. *sinuosum*, and *A. skutchii*. The *psbJ–petA* spacer contained an 8-bp deletion only in the samples of *A. skutchii* and *A. grandidentatum* var. *sinuosum* from Coahuila and Nuevo León. From the total number of chloroplast characters, 1,786 (81%) characters were constant, 303 (13.7%) variable characters were parsimony uninformative, and 115 (5.2%) characters were parsimony informative. The uncorrected pairwise distance between taxa ranged from 0.1% among *A. binzayedii–A. skutchii–A. saccharum–A. grandidentatum* var. *sinuosum* to 0.8%–1.5% between *A. grandidentatum* and the rest of the *Saccharodendron* members.

The likelihood values of the trees retained in Bayesian analyses of the ITS and chloroplast datasets ranged from –6,344.82 to –6,462.66 and from –4,128.88 to –4,133.22 (full range), respectively. The resulting maximum clade credibility trees are given in Fig. 14 and 15. The *Acer* clade (ITS dataset posterior probability [PP] = 0.80, chloroplast PP = 1.00) contained a well-supported

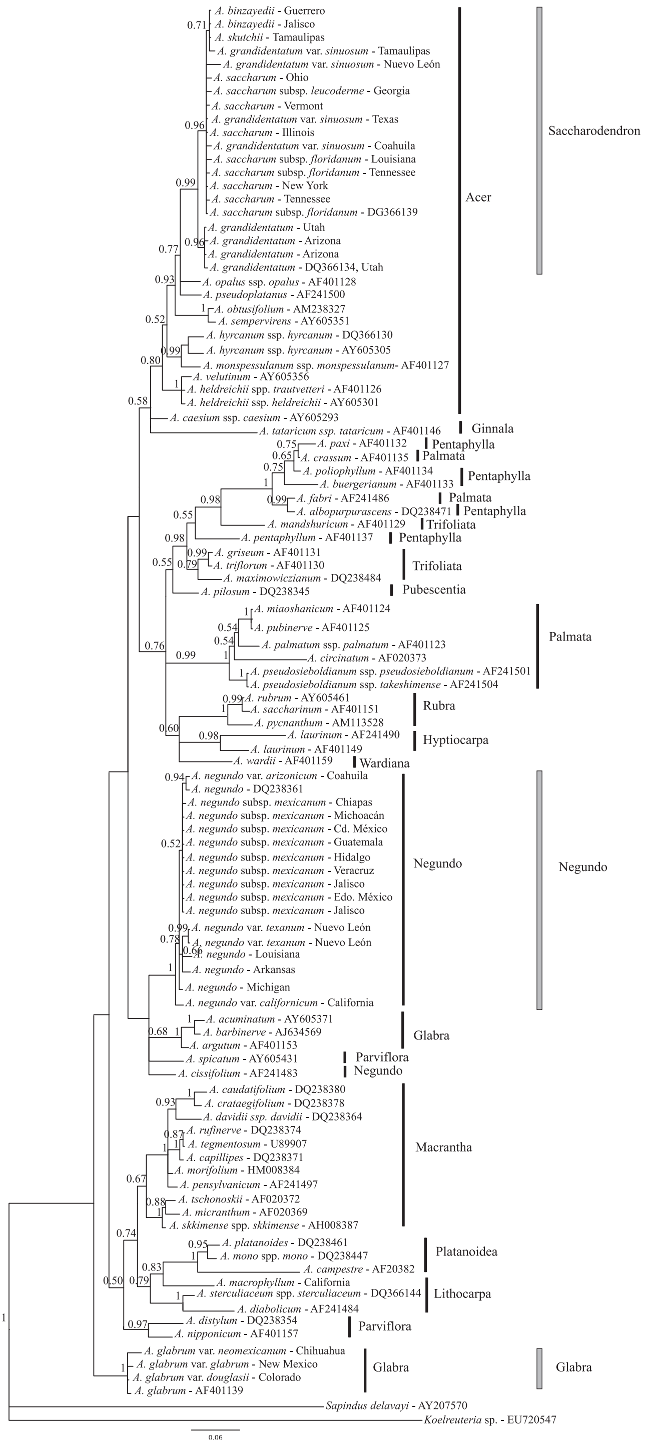

FIG. 14. Maximum clade credibility Bayesian tree based on the nuclear ribosomal DNA internal transcribed spacer sequence data. Numbers at the nodes indicate posterior probability values. Sections are indicated with black bars (following van Gelderen *et al*. 1994) and series are indicated with grey bars only for the species present in Mexico and Central America.

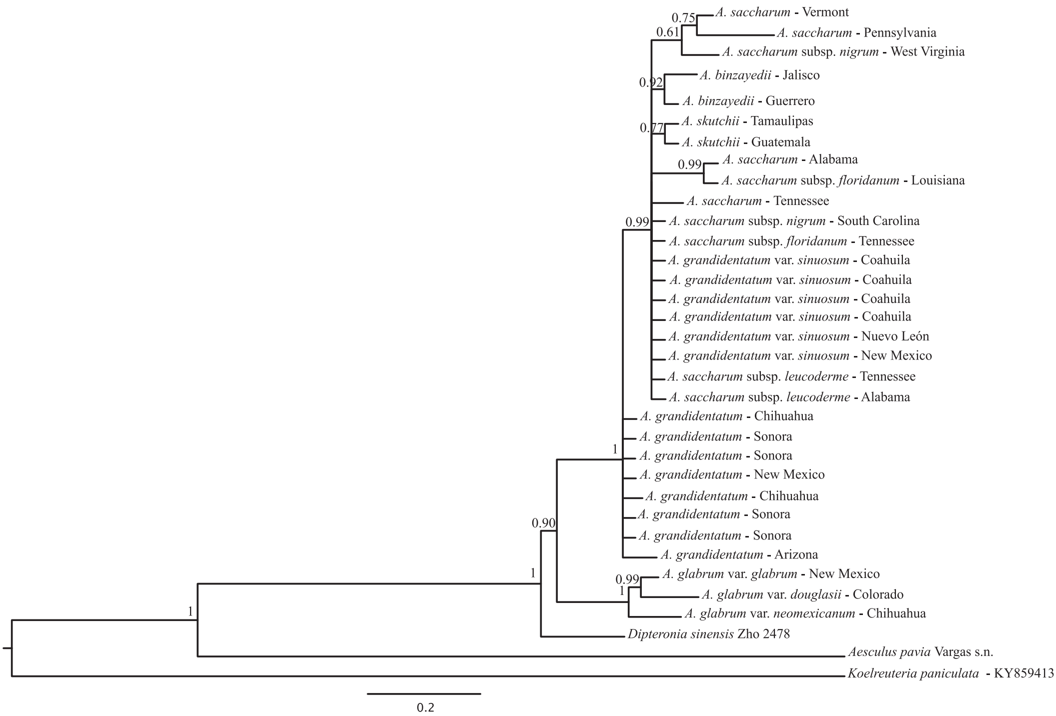

FIG. 15. Maximum clade credibility Bayesian tree based on the *ndhF–rpl32R* and *psbJ–petA* sequence data. Numbers at the nodes indicate posterior probability values.

clade (PP = 0.99), consisting of the species from the *Saccharodendron* series (Fig. 14). In the ITS tree topology, *A. grandidentatum* from the western USA and western Mexico were separated in a sister clade. Within the eastern North American and Mexican sugar maple clade, the relationships were not resolved using the ITS-based phylogeny (Fig. 14). *Acer binzayedii* formed a clade separate from the rest of sugar maples in the chloroplast phylogeny. However, the polytomies, which were also present in other *Saccharodendron* members in the chloroplast tree, did not allow the resolution of their relationships (Fig. 15).

A clade containing American members of *Negundo* received high support (PP = 1). This clade was examined using only the ITS marker because it was not possible to obtain good quality sequences of the chloroplast regions. Only two clades, one containing the species from western Mexico and the other containing the populations from eastern Mexico received a high support (PP = 0.94 and PP = 0.99, respectively) (Fig. 14). The Mexican populations of *A. negundo* subsp. *mexicanum* grouped together in a clade sister to the populations from Coahuila (*A. negundo* var. *arizonicum*). Eastern Mexican populations of *A. negundo* var. *texanum* grouped in a clade sister to *A. negundo* populations from Louisiana and Arkansas (Fig. 14). However, both *A. negundo* subsp. *mexicanum* and *A. negundo* var. *texanum* clades had a low support.

All *A. glabrum* members formed a highly supported clade in the topology inferred from both the ITS (PP = 0.99) and chloroplast (PP = 1) sequences (Fig. 14, 15). Within this clade in the chloroplast-based topology, the accession of the Mexican population of *A. glabrum* var. *neomexicanum* was retrieved as sister to the clade containing *A. glabrum* var. *glabrum* and *A. glabrum* var. *douglasii* (PP = 1) (Fig. 15).

Discussion. *Acer caesium* Wall. ex Brandis, a Eurasian member of the section *Acer*, was retrieved as sister to the *Acer* core clade, which is consistent with previous studies (Grimm *et al.* 2006, 2007; Li *et al.* 2019). Other taxa such as *Acer opalus* Mill. and *Acer sempervirens* L. (also from Eurasia), members of the *Monspessulana* series, grouped with the *Acer* section. Thus, the clade division of the Eurasian members was in agreement with the groups identified by Grimm *et al*. (2006).

Within the *Saccharodendron* series (includes the North American species), *A. grandidentatum* was retrieved as sister to the clade with eastern USA species of the series (Fig. 14, 15). The apparent *A. grandidentatum* lineage from the western USA was also recovered using ITS data by Grimm *et al*. (2007). Considering the ITS sequence variants recovered from *A. grandidentatum*, Grimm *et al*. (2007) suggested a western North American origin of the *Saccharodendron* group, independent of the Eurasian taxa. However, fossils of *Acer pseudo-ginnala* Tanai et Onoe and *Acer yamanae* Tanai et Ozaki from the Miocene found in East Asia are similar to the extant *A. saccharum* and *A. saccharum* subsp. *nigrum* (Tanai 1983), questioning the postulation by Grimm *et al*. (2007) about the independent origin of this group.

The Mexican and Guatemalan populations of *A. skutchii*, *A. binzayedii*, and *A. grandidentatum* var. *sinuosum* formed a clade in the Bayesian topology based on the ITS sequence data (Fig. 14). Gene flow among the populations of *A. grandidentatum* var. *sinuosum* and *A. skutchii,* located in Texas and Tamaulipas, respectively, could have occured during the last glacial periods. However, *A. binzayedii* grouped in the chloroplast-based topology, thus indicating the distinction of the populations from western Mexico as a separate lineage, a pattern found also in a previous study (Vargas-Rodriguez *et al*. 2015). *Acer saccharum* and other species of the *Saccharodendron* group (from eastern North America) formed a weakly supported polytomous clade. There is the possibility that some of the members of the eastern USA group of *Saccharodendron* can be treated as subspecies (Desmarais 1952, Murray 1975). To resolve their relationships, more individuals from different populations, additional molecular markers, and other genomic regions may required to be explored. For instance, the nuclear loci obtained with the anchored hybrid enrichment method used by Li *et al*. (2019) could provide better resolution. Considering these previous limitations, this study uses morphological characters to propose taxonomic statuses, with the conservative support of the phylogenetic species concept.

Although the intrasectional relationships within *Negundo* were not fully resolved, accessions from central Mexico (*A. negundo* subsp. *mexicanum*) formed a clade with those of *A. negundo* var. *texanum. Acer negundo* var. *californicum* was retrived as sister to the rest of the *Negundo* clade. The *A. glabrum* group from western USA and from northern Mexico formed a separate lineage; the same pattern was reported in previous studies (Suh *et al*. 2000, Tian *et al*. 2002, Grimm *et al*. 2006) (Fig. 14).

Intersectional and intrasectional relationships of *Acer* have been examined using chloroplast noncoding regions, but the phylogenetic resolution has been poor (Hasebe *et al*. 1998, Xin *et al*. 2002, Li *et al*. 2006, Zhang *et al*. 2010). Some of those regions have shown no variation at the intraspecific level (Renner *et al*. 2007) and provided little phylogenetic resolution within the clades of *Prunus* (Rosaceae) (Shaw and Small 2005). Using the molecular markers *psbJ–petA* and *rpl32R–ndhF* (Shaw *et al*. 2007), a well-supported *A. saccharum* lineage from the midwestern USA was identified (Vargas-Rodriguez *et al*. 2015), whereas the relationships within the eastern USA sugar maple species did not receive strong support. Poor resolution might result from the lack of sequence variability, invoking the need to examine other gene regions or use next-generation sequencing techniques (Wen *et al*. 2015).

The nuclear ribosomal DNA (nrDNA) ITS has been either an unsuitable marker or the best option for plant phylogenetic reconstruction. The ITS is repeated in many copies producing paralogs as result of concerted evolution, with some of the paralogs displaying polymorphisms as a consequence of hybridization (Xiao *et al*. 2010). Incomplete lineage sorting due to recent species divergence may also produce conflicting signals in the nuclear region. Nevertheless, the nrDNA ITS marker has been the best choice for DNA identification of *Alnus* species (Ren *et al*. 2010), and it was superior to some of the chloroplast regions used in barcoding (China Plant BOL Group 2011). Within the *Acer* genus, the nrDNA ITS has been used as a phylogenetic marker and it has recovered limited support for some intrasectional relationships (Grimm *et al*. 2006, Buerki *et al*. 2010), but good support for intersectional relationships (Grimm *et al*. 2006, Harris *et al*. 2017).

Hybridization among species from the eastern USA in the *Saccharodendron* series could be frequent (van Gelderen *et al*. 1994, Grimm *et al*. 2007). Species delimitation in this group will require the identification of appropriate nuclear and chloroplast regions for recovering intraspecific variation (Renner *et al*. 2007, Wen *et al*. 2015, Li *et al*. 2019). It will also allow detection of morphologically cryptic species within highly variable series. In addition, gene flow should be examined to discriminate between intraspecific and interspecific differences for this complex group (Hey and Pinho 2012).

The morphological evidence indicated the following species growing in Mexico and Central America: *A. negundo* subsp. *mexicanum*, present in Mexico and Central America; *A. negundo* var. *arizonicum* in northwestern Mexico; *A. negundo* var. *texanum* in northeastern Mexico; *A. glabrum* var. *neomexicanum* growing only in northwestern Mexico; *A. grandidentatum* in northwest Mexico; *A. grandidentatum* var. *sinuosum* occurring in northeastern Mexico; *A. skutchii* from eastern and southern Mexico and Guatemala; and the recently described *A. binzyedii* endemic to western Mexico. The varieties *A. negundo* var. *arizonicum* and *A. negundo* var. *texanum* are reported for the first time in Mexico.

The *Acer* species discussed here are scattered throughout the studied region, following the distribution of the main mountain chains (*e.g*., Fig. 2, 9, 10). Their populations are disjunct and, in some cases, separated by hundreds of kilometers (*e.g*., Fig. 7, 12, 13). *Acer negundo* subsp. *mexicanum* occurs in many sites throughout Mexico and Central America, albeit at a very low abundance in all locations (Fig. 2). The subspecies has an ample elevational range and it is mainly present along creeks in pine-oak forests or cloud forests. The subspecies is valued for restoration of riparian ecosystems in Mexico. On the other hand, the *A. negundo* varieties *arizonicum* and *texanum* are restricted and unique to two disjunct regions of northern Mexico (Fig. 4, 5). *Acer glabrum* var. *neomexicanum* has been located at only two sites in northwestern Mexico, but in the USA the subspecies covers a larger area (Fig. 7). It is usually observed in conifer and hardwood forests. *Acer grandidentatum* has been recorded in the Sierra Madre Occidental and *A. grandidentatum* var. *sinuosum* in the Sierra Madre Oriental. Both are typically found in canyon bottoms and ravines with steep slopes. *Acer binzayedii* and *A. skutchii* grow along creeks, in cloud forests at higher elevations, and in ravines with small populations. This updated distribution and population sizes are smaller than those proposed by Gibbs and Chen (2009). These last two species are critically endangered according to the IUCN Red List (Vargas-Rodriguez 2017, Vargas-Rodriguez *et al*. 2017a).

Acer has a scattered distribution in Middle America, growing in high-elevation temperate or cloud forests. The presence of *Acer*, as well as other temperate taxa (*i.e*., *Fagus* sp. L., *Liquidambar* sp., *Tilia* sp.) at the most southern geographical range has been associated with lower temperatures during glacial periods that allowed them to expand their ranges to lower latitudes (Graham 1999). Warmer temperatures during interglacials resulted in fragmented populations, reducing connectivity among them, thus promoting divergence from more northern populations (Vargas-Rodriguez *et al*. 2015). Hence, *Acer* species, as well other temperate taxa in Middle America, are now considered relicts, with separate lineages from their more northern populations, and are probably facing different environmental pressures under a changing climate.

Literature Cited

Ackerly, D. D. and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in Maples (*Acer*). American Naturalist 152: 767–791.

Anderson, E. and L. Hubricht. 1938. The American sugar maples. I. Phylogenetic relationships, as deduced from a study of leaf variation. Botanical Gazette 100: 312–323.

[APG] Angiosperm Phylogeny Group. 1998. An ordinal classification for the families of flowering plants. Annals of the Missouri Botanical Garden 85: 531–553.

[APG] Angiosperm Phylogeny Group . 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society 141: 399–436.

[APG] Angiosperm Phylogeny Group . 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161: 105–121.

[APG] Angiosperm Phylogeny Group . 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1–20.

Ayensu, E. S. 1967. Aerosol OT solution—An effective softener of herbarium specimens for anatomical study. Stain Technology 42: 155–156.

Brizicky, K. 1963. Aceraceae in genera Sapindales. Journal of the Arnold Arboretum 44: 481–494.

Buerki, S., P. Lowry, N. Alvarez, S. G. Razafimandimbison, P. Küpfer, and M. W. Callmander. 2010. Phylogeny and circumscription of Sapindaceae revisited: Molecular sequence data, morphology and biogeography support recognition of a new family, Xanthoceraceae. Plant Ecology and Evolution 143: 148–159.

Buerki, S., F. Forest, P. Acevedo-Rodríguez, M. W. Callmander, J. A. A. Nylander, M. Harrington, I. Sanmartín, F. Küpfer, and N. Alvarez. 2009. Plastid and nuclear DNA markers reveal intricate relationships at subfamilial and tribal levels in the soapberry family (Sapindaceae). Molecular Phylogenetics and Evolution 51: 238–258.

Cabrera-Rodríguez, L. 1985. Aceraceae. Flora de Veracruz. Instituto Nacional de Investigaciones sobre Recursos Bióticos, Xalapa, Veracruz, Mexico. 7 pp.

Calderón de Rzedowski, G. 2001. Familia Aceraceae. Flora del Bajío y de regiones adyacentes. Instituto de Ecología A. C., Pátzcuaro, Michoacán, Mexico. 9 pp.

China Plant BOL Group. 2011. Comparative analysis of a large dataset indicates that internal transcribed spacer (ITS) should be incorporated into the core barcode for seed plants. Proceedings of the National Academy of Sciences of the United States of America 108: 19641–19646.

Correll, D. S. and M. C. Johnston. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner, TX. 1881 pp.

Cronquist, A. J., N. H. Holmgren, and P. K. Holmgren. 1997. Intermountain Flora: Vascular Plants of the Intermountain West, USA. Volume 3, Part A, Subclass Rosidae (Except Fabales). New York Botanical Garden, New York, NY. 446 pp.

de Jong, P. C. 1976. Flowering and Sex Expression in *Acer* L. a Biosystematic Study. Mededelingen Landbouwhogeschool, Wageningen, Netherlands. 201 pp.

Delendick, T. 1981. A systematic review of the Aceraceae. Ph.D. thesis. City University of New York, New York, NY. 693 pp.

Desmaris, Y. 1952. Dynamics of leaf variation in the sugar maples. Brittonia 7: 347–387.

Diggs, G. M., B. L. Lipscomb, and R. J. O'Kennon. 1999. Illustrated Flora of North Central Texas. Botanical Research Institute of Texas, Fort Worth, TX. 1626 pp.

Drummond, A. J., M. A. Suchard, X. Dong, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29: 1969–1973.

Ellis, W. H. 1963. Revision of *Acer* section *Rubra* of eastern North America, excluding *Acer saccharinum* L. Ph.D. thesis. University of Tennessee, Knoxville, TN. 195 pp.

Gibbs, D. and Y. Chen. 2009. The Red List of Maples. Botanic Gardens Conservation International, Richmond, UK. 40 pp.

González-Espinosa, M., J. A. Meave, F. G. Lorea-Hernández, G. Ibarra-Manríquez, and A. C. Newton. 2011. The Red List of Mexican Cloud Forest Trees. Flora & Fauna International, Cambridge, UK. 124 pp.

Graham, A. 1999. The Tertiary history of the northern temperate element in the northern Latin America biota. American Journal of Botany 86: 32–38.

Grimm, G. W., T. Denk, and V. Hemleben. 2007. Evolutionary history and systematics of *Acer* section *Acer*—A case study of low-level phylogenetics. Plant Systematics and Evolution 267: 215–253.

Grimm, G. W., S. S. Renner, A. Stamatakis, and V. Hemleben. 2006. A nuclear ribosomal DNA phylogeny of *Acer* inferred with maximum likelihood, splits graphs, and motif analysis of 606 sequences. Evolutionary Bioinformatics 2: 7–22.

Harrington, M. G., K. J. Edwards, S. A. Johnson, M. W. Chase, and P. A. Gadek. 2005. Phylogenetic inference in Sapindaceae sensu lato using plastid matK and rbcL DNA sequences. Systematic Botany 30: 366–382.

Hasebe, M., T. Ando, and K. Iwatsuki. 1998. Infrageneric relationships of maple trees based on the chloroplast DNA restriction fragment length polymorphisms. Journal of Plant Research 111: 441–451.

Hey, J. and C. Pinho. 2012. Population genetics and objectivity in species diagnosis. Evolution 66: 1413–1429.

[IUCN] International Union for Conservation of Nature and Natural Resources. 2012. IUCN Red List Categories and Criteria: Version 3.1. IUCN, Gland, Switzerland and Cambridge, UK. 32 pp.

Justice, D. E. C. 1995. The systematics of Rocky Mountain maple, *Acer glabrum* Torr. M.Sc. thesis. The University of British Columbia, Vancouver, BC, Canada. 157 pp.

Keller, A. C. 1942. *Acer glabrum* and its varieties. American Midland Naturalist 27: 491–500.

Krause, C. R. 1982. Differentiation of black and sugar maple cultivars with scanning electron microscopy. Journal of the American Society For Horticultural Science 107: 186–188.

Li, J., J. Yue, and S. Shoup. 2006. Phylogenetics of *Acer* (Aceroideae, Sapindaceae) based on nucleotide sequences of two chloroplast non-coding regions. Harvard Papers in Botany 11: 101–115.

Li, J., M. Stukel, P. Bussies, K. Skinner, A. R. Lemmon, E. M. Lemmon, K. Brown, A. Bekmetjev, and N. G. Swenson. 2019. Maple phylogeny and biogeography inferred from phylogenomic data. Journal of Systematics and Evolution doi.org/10.1111/jse.12535.

Maddison, D. R. and W. P. Maddison. 2000. MacClade 4: Analysis of Phylogeny and Character Evolution. Release Version 4.08 for OSX. Sinauer Associates, Inc., Sunderland, MA.

McClain, A. M. and S. R. Manchester. 2001. *Dipteronia* (Sapindaceae) from the Tertiary of North America and implications for the phytogeographic history of the Aceroideae. American Journal of Botany 88: 1316–1325.

Murray, A. E. 1970. A monograph of the Aceraceae. Ph.D. thesis. Pennsylnavia State University, Pennsylvania, PA. 322 pp.

Murray, A. E. 1975. North American maples. Kalmia 7: 1–19.

Murray, A. E. 1980a. Guatemalan maples. Kalmia 10: 3–4.

Murray, A. E. 1980b. Mexican maples (arces mexicanos). Kalmia 10: 5–8.

Murray, A. E. 1981. *Acer* of North America. Kalmia 11: 3–8.

Nicholson, G. 1881. The Kew Arboretum. The maples. I–XVI. Gardener's Chronicle 15: 10–788.

NYLANDER, J. A. A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

R CORE TEAM. 2013. R: A language and environment for statistical computing. Retrieved August 3, 2013 from R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

RAMBAUT, A. 2012. FigTree v1.4, graphical viewer of phylogenetic trees. Retrieved August 3, 2012 from University of Edinburgh. <http://tree.bio.ed.ac.uk/software/figtree/>.

RAMBAUT, A., M. A. SUCHARD, W. XIE, AND A. J. DRUMMOND. 2014. Tracer v1.6. Retrieved August 3, 2014 from Institute of Evolutionary Biology, University of Edinburgh. <http://beast.bio.ed.ac.uk/Tracer>.

REHDER, A. 1927. Manual of Cultivated Trees and Shrubs. Collier Macmillan, New York, NY. 966 pp.

REHDER, A. 1933. New species, varieties, and combinations. *Acer* sect. Macrantha. Journal of the Arnold Arboretum 14: 211–212.

REHDER, A. 1949. Bibliography of Cultivated Trees and Shrubs Hardy in the Cooler Temperate Regions of the Northern Hemisphere. Harvard University, Jamaica Plain, Boston, MA. 825 pp.

REN, B. Q., X. G. XIANG, AND Z. D. CHEN. 2010. Species identification of *Alnus* (Betulaceae) using nrDNA and cpDNA genetic markers. Molecular Ecology Resources 10: 594–605.

RENNER, S. S., L. BEENKEN, G. W. GRIMM, A. KOCYAN, AND R. E. RICKLEFS. 2007. The evolution of dioecy, heterodichogamy, and labile sex expression in *Acer*. Evolution 61: 2701–2719.

RONQUIST, F. AND J. P. HUELSENBECK. 2011. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

SARGENT, C. S. 1891a. Notes on North American trees—XXV. Garden and Forest 4: 147–148.

SARGENT, C. S. 1891b. Silva of North America: A description of the trees which grow naturally in North America exclusive of Mexico. Vol. 2. Houghton Mifflin, Boston, MA. 117 pp.

SARGENT, C. S. 1902. Silva of North America: A description of the trees which grow naturally in North America exclusive of Mexico. Houghton Mifflin 13: 7–11.

SARGENT, C. S. 1919. Notes on North American trees. Botanical Gazette 67: 233–241.

SELA, I., H. ASHKENAZY, K. KATOH, AND T. PUPKO. 2015. GUIDANCE2: Accurate detection of unreliable alignment regions accounting for the uncertainty of multiple parameters. Nucleic Acids Research 43: W7–W14.

SHAW, J. AND R. L. SMALL. 2005. Chloroplast DNA phylogeniy and phylogeography of the North American plums (*Prunus* subgenus *Prunus* section *Prunocerasus*, Rosaceae). American Journal of Botany 92: 2011–2030.

SHAW, J., E. B. LICKEY, E. E. SCHILLING, AND R. SMALL. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. American Journal of Botany 94: 275–288.

STANDLEY, P. C. AND J. A. STEYERMARK. 1949. Flora of Guatemala. Fieldiana 24: 230–233.

SUH, Y., K. HEO, AND C. W. PARK. 2000. Phylogenetic relationships of maples (*Acer* L.; Aceraceae) implied by nuclear ribosomal sequences. Journal of Plant Research 113: 193–202.

TANAI, T. 1983. Revisions of Tertiary *Acer* from East Asia. Journal of the Faculty of Science Hokkaido University Series IV 20: 291–390.

THIERS, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/

TIAN, X., Z. H. GUO, AND D. Z. LI. 2002. Phylogeny of Aceraceae based on ITS and trnL–F data sets. Acta Botanica Sinica 44: 714–724.

URBATSCH, L. E., B. G. BALDWIN, AND M. J. DONOGHUE. 2000. Phylogeny of the coneflowers and relatives (Heliantheae: Asteraceae) based on the nuclear rDNA internal transcribed spacer (ITS) sequences and chloroplast DNA restriction site data. Systematic Botany 25: 539–565.

VAN GELDEREN, D. M., P. C. DE JONG, AND H. J. OTERDOOM. 1994. Maples of the World. Timber Press, Portland, OR. 458 pp.

VARGAS-RODRIGUEZ, Y. L. 2011. Sapindaceae: *Acer saccharum* subsp. *skutchii*, *Acer negundo* subsp. *mexicanum*, pp. 1–149. *In* M. González, J. Meave, F. Lorea, G. Ibarra, and A. Newton, eds. The Red List of Mexican Cloud Forest Trees. Fauna & Flora International, Botanical Gardens Conservation International, The Global Trees Campaign, The IUCN/SSC Global Tree Specialist Group, London, UK.

VARGAS-RODRÍGUEZ, Y. L. 2017. *Acer binzayedii*. The IUCN Red List of Threatened Species 2017: e.T112788439A112788448. <http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T112788439A112788448.en>. Retrieved November 10 2017.

VARGAS-RODRIGUEZ, Y. L. AND W. J. PLATT. 2012. Remnant sugar maple (*Acer saccharum* subsp. *skutchii*) populations at their range edge: Characteristics, environmental constraints and conservation implications in tropical America. Biological Conservation 150: 111–120. doi.org/10.1016/j.biocon.2012.03.006.

VARGAS-RODRÍGUEZ, Y. L., D. CROWLEY, M. BARSTOW, AND M. C. RIVERS. 2017a. *Acer skutchii*. The IUCN Red List of Threatened Species 2017: e.T103451945A103451954. <http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T103451945A103451954.en>. Retrieved November 10 2017.

VARGAS-RODRIGUEZ, Y.L., W. J. PLATT, L. E. URBATSCH, AND D. W. FOLTZ. 2015. Large scale patterns of genetic variation and differentiation in sugar maple from tropical Central America to temperate North America. BMC Evolutionary Biology 15: 257. doi.org/10.1186/s12862-015-0518-7.

VARGAS-RODRIGUEZ, Y. L., L. E. URBATSCH, V. KARAMAN-CASTRO, AND B. L. FIGUEROA-RANGEL. 2017b. *Acer binzayedii* (Sapindaceae) a new maple species from Mexico. Brittonia 69: 246–252.

WELSH, S. L., N. D. ATWOOD, L. C. HIGGINS, AND S. GOODRICH. 1987. A Utah flora. Great Basin Naturalist Memoir 9: 1–894.

WEN, J., J. LIU, S. GE, Q. Y. XIANG, AND E. A. ZIMMER. 2015. Phylogenomic approaches to deciphering the tree of life. Journal of Systematics and Evolution 53: 369–370.

WESMAEL, A. 1890. Revue critique des éspeces du genre *Acer*. Bulletin de la Société Royale de Botanique de Belgique 29: 17–65.

WHITE, T. J., T. BURNS, S. LEE, AND J. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics, pp. 315–322. *In* M. A. Innis, D. H. Gelfand, J. J. Sninsky, T. J. White, eds. PCR Protocols: A Guide to Methods and Applications. Academic Press, London, UK.

WOLFE, J. A. AND T. TANAI. 1987. Systematics, phylogeny, and distribution of *Acer* (maples) in the Cenozoic of western North America. Journal of the Faculty of Science, Hokkaido University Series IV 22: 1–246.

WOOTON, E. O. AND P. C. STANDLEY. 1915. Flora of New Mexico. Contributions from the United States Herbarium 19: 1–794.

XIAO, L. Q., M. MOLLER, AND H. ZHU. 2010. High nrDNA ITS polymorphism in the ancient extant seed plant *Cycas*: Incomplete concerted evolution and the origin of pseudogenes. Molecular Phylogenetics and Evolution 55: 168–177.

XIN, T., C. ZHEN-HUA, AND L. DE-ZHU. 2002. Phylogeny of Aceraceae based on ITS and trnL–F data sets. Acta Botanica Sinica 44: 714–724.

ZHANG, Z., C. LI, AND J. LI. 2010. Conflicting phylogenies of Section *Macrantha* (*Acer*, Aceroideae, Sapindaceae) based on chloroplast and nuclear data. Systematic Botany 35: 801–810.